EL PROCESO DE URBANIZACIÓN Y SU EFECTO EN LA DISPERSIÓN DE LAS AVES:

el caso de la lechucita de las vizcacheras (*Athene cunicularia*)

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El proceso de urbanización y su efecto en la dispersión de las aves: el caso de la lechucita de las vizcacheras (*Athene cunicularia*)

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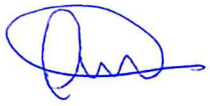

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First drawing of a Burrowing Owl

John James Audubon (1785-1851)

“A todos los que han ayudado a que esta tesis se haga realidad.”

Contents

I Prologue

II Chapters

III Appendix

IV Epilogue

V Agradecimientos

I| Prologue

List of Figures

General introduction

Chapter 1

Chapter 2

Figure 2. Effects of the breeding system (CB=cooperative breeding) and habitat on the breeding success (at least one chick per nest) and the productivity (number of fledglings per nest) of burrowing owls.

Figure 3. Model averaged estimates (Table 4) of survival probabilities of adults, rural and urban juveniles raised in cooperative breeding systems (black) and bi-parental systems (grey). Bars indicate the 90% interval confidences.

Chapter 3

Figure 1. (a) Proportion of burrowing owls showing site fidelity (1) or changing their breeding sites between successive years (0) in rural (grey bars) and urban (black bars) habitats. (b) For individuals changing their breeding sites, the accumulated proportion of dispersing urban (grey line) and rural (black line) individuals as a funciton of distance is also shown. The maximum dispersal distance observed is indicated by a point (grey and black, for urban and rural birds respectively). Vertical dashed lines show mean distances for urban (grey line) and rural (black line) birds.

Figure 2. (a) Factors affecting site fidelity among rural and urban burrowing owls (estimate ± 95% CI). Site fidelity was negatively related to individual behaviour (measured as flight initiation distances, FID) among rural individuals (b), while it was negatively related to conspecific density (measured as aggregation) among urban ones (c). Lines (black: rural, grey: urban) show the probability of remaining in the same breeding site for individuals with different FID and living at different conspecific densities. Dots (black: rural, white: urban) show predicted values.

List of Tables

Chapter 1

Chapter 2

Table 1. Modelling the effects of habitat (hab), productivity (product), and conspecific density (consp.density) on the probability to develop cooperative breeding in burrowing owls Athene cunicularia. Only models with an AICcweight >0 are shown (the complete series of model in SP1). df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc), w: Akaike weights.

Table 2. Relative importance of the breeding system (bi-parental vs. cooperative breeding) and habitat (rural vs. urban) on the body condition of chicks of burrowing owls *Athene cunicularia*. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models shown are those with w>0. Df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc), w: Akaike weights. hab=habitat; coop. breed.= cooperative breeding

Table 3. Testing the effects of the breeding system developed (bi-parental vs cooperative breeding) and habitat on fecundity of burrowing owls. Df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model *i* and that of the best model (*i.e*. the model with the lowest AICc), weight: Akaike weights. Null: null model.

Table 4. Modelling the effects of breeding system (bs), age (juv: juvenile; ad: adult) habitat (hab:habitat; urb:urban; rur:rural), and time (t) on survival. All models considered the effect of field effort on recaptures (SP4). Df= degrees of freedom; w=weight.

Chapter 3

Table 1. Alternative models (ΔBIC < 6) obtained to assess the relative importance of individual's traits (age, sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year t-1) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls Athene cunicularia. Models were run using information from individuals of known age (ringed as chicks). See Table S1 for alternative models obtained using the Akaike Information Criterion corrected for small sample sizes (AICc).

Table 2. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year t-1) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls Athene cunicularia. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models were run using all individuals of unknown age, as age has not received statistical support (see Table 1 and S1). Models shown are those used for model averaging (ΔBIC ≤ 6). See Table S2 for results obtained using the Akaike Information Criterion (ΔAICc < 6).

Table 3. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year t-1) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural burrowing owls Athene cunicularia with FID within the range of urban ones (5- 87m). Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models

shown are those used for model averaging (ΔBIC ≤ 6). See Table S3 for results obtained using the Akaike Information Criterion (ΔAICc < 6).

General discussion

Table 1. Summary of the main biological questions and results obtained in this thesis.

Resumen

Resumen

La urbanización del territorio se ha convertido en una de las mayores transformaciones del paisaje a nivel global, afectando profundamente a la biodiversidad presente donde las ciudades se asientan. Sin embargo, algunas especies son capaces de colonizar las ciudades e incluso prosperar en ellas. En los últimos años, un creciente interés se está focalizando en comprender qué caracteriza a los organismos que habitan ciudades, y cómo su conducta y dinámica poblacional se ve afectada por las transformaciones humanas del paisaje. La dispersión, un proceso fundamental con influencia en la demografía y la estructura poblacional, se encuentra entre los principales procesos ecológicos que puede verse alterado por la urbanización del territorio. Sin embargo, la investigación centrada en estudiar estrategias de dispersión en entornos urbanos es escasa.

Esta tesis se focaliza en la dispersión de la lechucita de las vizcacheras (*Athene cunicularia*) en la ciudad de Bahía Blanca (Argentina) y su entorno rural. Allí, un programa de monitoreo específico conducido entre 2006 y 2018 ha seguido aproximadamente 2500 territorios urbanos de esta especie y 3200 rurales, midiendo parámetros reproductores y anillando unos 2000 adultos y pollos. Este estudio a largo plazo se ha complementado con medidas de conducta. Específicamente, durante este tiempo se ha medido la variación individual respecto a la susceptibilidad a humanos. Este rasgo de personalidad se incluye en un conjunto de conductas donde se incluyen también la toma de riesgos, la agresividad, la exploración y la tendencia a dispersar, jugando un rol en la colonización de ciudades.

La hipótesis principal de esta tesis es que los individuos dispersan acorde a sus fenotipos, aunque sus decisiones de dispersión pueden estar también influenciadas por las heterogéneas presiones selectivas presentes en el área de estudio. Además, la coexistencia de diferentes estrategias de dispersión puede jugar un papel positivo o negativo en términos de “fitness” individual, con efecto potencial en la dinámica poblacional. Así, el objetivo de este estudio es comprender la influencia de características individuales (conducta, sexo y edad) y factores ambientales (calidad de

territorio natal y reproductor, presión de predadores y tipo de hábitat) en las estrategias de dispersión de la lechucita de las vizcacheras que habitan dos hábitats adyacentes pero profundamente diferentes, la ciudad y su zona rural inmediata. Además, evaluamos si las decisiones referentes a la dispersión influencian la eficacia biológica de los individuos en ambos hábitats en términos de reproducción y supervivencia.

En el primer capítulo nos hemos focalizado en la dispersión natal, los movimientos de los individuos juveniles entre su territorio de cría y aquel en el que se reproducirá por primera vez. Encontramos que las lechucitas urbanas dispersan menos que las rurales. Además, las hembras, los individuos atrevidos ("bold") y aquellos que han nacido en territorios de peor calidad dispersan más. Las hembras e individuos rurales que se instalan en territorios de cría más alejados de los de su origen obtienen beneficio en su primera reproducción, y esto se extiende a los dos sexos y hábitats cuando consideramos la productividad a lo largo de toda la vida. Como contrapartida las hembras que dispersan lejos sobreviven peor.

En el capítulo 2 exploramos la aparición de cría cooperativa, una estrategia poco habitual en esta especie de búho generalmente monógama. Mostramos que la cría cooperativa suele conformarse solo por tres adultos. El individuo adicional es generalmente un macho nacido la temporada previa en el mismo territorio que retrasa su dispersión y ayuda a sus padres. La colaboración de estos "ayudantes" puede incrementar el aprovisionamiento de comida, como lo evidencia el hecho de que los pollos nacidos en cría cooperativa tienen mejor condición física. La cría cooperativa aparece con mayor frecuencia en áreas más productivas en las que se agregan un mayor número de congéneres: la ciudad y zonas rurales de alta calidad. Además, territorios con ayudantes colaborando en tareas reproductoras obtienen mayor éxito reproductor. La descendencia criada en familias cooperativas tiene solo un ligero incremento en sus probabilidades de supervivencia al compararlo con juveniles nacidos en el sistema biparental habitual. En general, la supervivencia presenta variación temporal y el factor principal que influye en la supervivencia son la edad y el

hábitat: los adultos presentan mayor supervivencia que los jóvenes, que a su vez muestran mayor supervivencia en áreas urbanas que rurales.

Finalmente, el tercer capítulo se centra en la dispersión reproductora, los movimientos de los adultos entre territorios de cría en períodos reproductores consecutivos. Observamos que una parte significativa de la población se mantiene en el mismo nido. En caso de dispersar, los desplazamientos son más cortos que en la dispersión natal. Las hembras dispersan más que los machos y sus movimientos son más largos. Como también pasaba para la dispersión natal, los ejemplares urbanos muestran mayor fidelidad al territorio y dispersan distancias más cortas. En las zonas rurales, los individuos que sufren eventos de predación o fallan en la reproducción son más dados a dispersar. Sin embargo, los individuos más atrevidos ("bold") dispersan menos que los temerosos, probablemente porque son más capaces de hacer frente a potenciales perturbaciones sufridas durante el período de reproducción sin que ello les incite a dispersar. La influencia del comportamiento en la dispersión desaparece en el hábitat urbano, donde solo se observa que los individuos nacidos en territorios más ocupados por conspecíficos dispersan más.

Summary

Summary

Urbanization has become one of the greatest landscape transformations at global level, deeply affecting the biodiversity present where cities settle. However, some species are able to thrive and even prosper in urban ecosystems. In recent years, a growing interest is focusing in understand what characterizes the organisms inhabiting cities, and how their behavior and their population dynamics can cope with human transformed environments. Dispersal, a fundamental process with influence on the demography and the structure of populations, is among the main ecological processes that may be altered by the urbanization. However, research devoted to study the dispersal strategies of animals in urban environments is scarce.

This thesis focuses on the dispersal of the burrowing owl (*Athene cunicularia*) in the city of Bahía Blanca (Argentina) and its rural surroundings. There, a specific monitoring program conducted annually from 2006 to 2018 have surveyed ca. 2500 urban and ca. 3200 rural nests of this species, recording reproductive parameters and marking ca. 2000 adults and chicks. This long-term study has been complemented with measurements of burrowing owls behavior. Specifically, we have recorded the individual variation in the susceptibility to humans. This personality trait is included within a range of behaviors that encompasses risk taking, aggressiveness, and exploration and dispersal propensity, also playing a role in the colonization of cities.

The main hypothesis of this thesis is that individuals disperse according to their phenotypes, although their dispersal decisions may be also influenced by the heterogeneous selective pressures observed in the study area. Furthermore, the coexistence of different dispersal strategies may play a positive or negative role in term of individual fitness, with potential effect in the population dynamic. Thus, the aim of this study is to understand the influence of individual cues (behavior, sex and age) and environmental factors (quality of natal and breeding zones, predation pressure and habitat type) in dispersal strategies of burrowing owls in adjacent but deeply different habitats, the city and their immediate rural area. Moreover, we assess

whether dispersal decisions influence the biological effectiveness of individuals in both habitats in terms of reproductive parameters and survival.

In the Chapter 1 we focus on natal dispersal, movement of juveniles between its birth site and the site where it first reproduces. We find that urban burrowing owl disperse less than rural ones. In addition, females, bold individuals and those born in poor quality territories disperse more. Females and rural individuals who settle far from their familiar territories improve their reproductive output in their first breeding attempt, and this extends to both sexes and habitats when we consider productivity throughout the entire life. On the contrary, females that disperse farther show lower local survival.

In the Chapter 2 we explore the development of cooperative breeding, an uncommon strategy in this monogamous owl. We show that cooperative families are mainly composed by three adults. The extra individuals are generally males born the last breeding season in the same territory delaying their dispersal to help their parents. The collaboration of these helpers can increase food provisioning, as evidenced by the fact that chicks born in cooperative breeding have a better physical condition. Cooperative breeding appears more frequently in highly productive areas in which a greater number of conspecifics aggregate: the city and high quality rural areas. Furthermore, territories with helpers collaborating in reproductive tasks show higher breeding success. The offspring raised in cooperative families have only a slight increase in their survival probabilities compared with juveniles raised in common pairs. Survival show temporal variations and the main factors driving survival differences are age and habitat: adults show higher survival than juveniles, which show a higher survival in urban than in rural habitats.

Finally, in the Chapter 3 focuses we study breeding dispersal, the movements of adults between breeding territories in subsequent breeding seasons. We observe that a significant part of the population remains faithful to the same territory. When disperse, the distances covered are shorter than those observed in the natal dispersal. In general, females disperse more frequently and they travel longer distances than males. Again, urban individuals are less prone to disperse, settling at shorter distances

from the previous nest. In rural areas, individuals that suffer predatory events or breeding failure in a territory disperse more. However, bold individuals disperse less than those fearful, probably due to their higher ability to cope with the disturbances suffered during the breeding period. The influence of behavior disappears in the urban environment, where it is only observed that individuals born in territories where more conspecifics are aggregated disperse more than those born in less occupied areas.

General introduction

General introduction

A brief approach to the cities

Urbanization has emerged as one of the most profound and lasting transformations of the landscape that humans are carrying out (McKinney 2006). Although a century ago only the 16% of people lived in cities, today urban environments cover approximately the 7% of the ice-free territories of the planet, and for the first time in history, more than half of the world's population lives in cities (Ellis and Ramankutty 2008). The inexorable trend towards global urbanization continues to rise, and some estimates suggest that almost 70% of humanity will live in cities by 2050 (United Nations 2007).The presence of cities in a landscape entails abiotic and biotic modifications that differentiate urban environments from any other ecosystem (Pickett et al. 2001). This includes the own physical environment of cities, which often makes its presence incompatible with other types of land uses (Antrop 2004). Furthermore, cities are characterized by higher temperatures compared with their surrounding ecosystems due to the "heat island effect" (Oke 1995) and by high levels of noise, light and chemical pollution (Hölker et al. 2010; Bichet et al.2013; Francis and Barber 2013).

In short, the gradual urbanization of the world represents a novel scenario that confront us with new challenges, mainly linked to understand how these changes in the organization of human societies are related to nature (Bettencourt et al. 2007). In this sense, scientists, conservationists and politicians consider that understanding properly the patterns that explain how plants and animals cope with cities is a priority within urban planning and biodiversity conservation (Dearborn and Kark 2010; Aronson et al. 2014).

The emergence of the urban ecology

The biodiversity of cities has not captured the attention of researchers until recent times. Traditionally, urbanized landscapes have been classified as “biological deserts”, homogeneous and poor sites in which processes of local extinction are the rule (Clergeau et al. 2006; Ortega-Alvárez and MacGregor-Fors 2009; Faeth et al. 2011). However, in the last decades the interest toward urban biodiversity has increased, revealing a more complex world than had been thought until now.

In this way, the recent effort devoted to understand how nature thrive in urbanized areas shows that a great variety of species can survive and proliferate in such environments, reaching population densities even higher than in their original habitats (Aronson et al. 2014; Rebolo-Ifrán et al. 2017; Callaghan et al. 2019). Indeed, we begin to discover that urban areas can serve as refuge for endangered species with a marked decline in their natural range, what make cities an unexpected habitat with a role for the conservation of certain species (Ives et al. 2016; Luna et al. 2018; Löki et al. 2019).

In this scenario, the urban ecology has become an area that has gained enormous interest in recent times (McDonnell and Niemelä 2011). Thus, since its emergence in the second part of the 20th century, the perspective that urban ecologists have obtained by combining different approaches has promoted the understanding of a great variety of factors involved in the interaction of biodiversity with cities (McDonnell and Niemelä 2011; Pickett et al. 2001; Wu 2014). At the beginning, the predominant topic for urban ecology was the acquisition of a general knowledge concerning the diversity of species occurring in cities, together with the environmental characteristics explaining their presence (Donnelly and Marzluff 2004; Tratalos et al. 2007; Ahern 2013). Moreover, another very active research line focus on the potential effects of urban pollution -light, acoustics, chemical, etc. – on the species inhabiting human dominated areas (Slabbekoorn and Peet 2003; Davies et al. 2013). Biodiversity at cities is been used even as ecological indicators (biomonitors) of pollutants related to urban areas (Rucandio et al. 2011; Llop et al. 2012; Herrera-Dueñas et al. 2014).

Cities represent a stimulating scenario for researchers, allowing to disentangle which traits favor certain species and/or individuals to exploit niches that they have never before faced in their evolutionary history (McKinney 2002). In this sense, nowadays, researchers are focusing on the basis of the process of colonization and urban settlement itself, that is, why some species become urban and how the process is (Kark et al. 2007; Møller and Ibáñez-Álamo 2012; Payo-Payo et al. 2017). Growing evidences suggest that the species thriving in cities have greater environmental tolerance (Bonier et al. 2007), and possess relatively higher brains (Maklakov et al. 2011). In addition, at species level, urban animals are typically generalists in terms of diet and breeding preferences (Kark et al. 2007; Callaghan et al. 2019), as well as reproductively prolific (Santini et al. 2019). However, today is known that not all the individuals of a species or population are able to successfully colonize cities: only those with certain genotypic and phenotypic traits are able to thrive in urban environments (Evans et al. 2009). For example, urban individuals typically show less fear to people and greater tolerance to human disturbances -and the frenetic activities and novelties- that characterize the cities (Lowry et al. 2013). On the contrary, shy individuals do not respond properly to the urban pressure, showing disadvantages that may prevent them from establish in urban environments (Møller 2009; Carrete et al. 2016; Carrete and Tella 2017).

Finally, cities expose the organisms living within their influence to new selective pressures that are leading to rapid changes in urban organisms (Alberti et al 2017; Johnson and Munshi-South 2017). In this way, taxa as diverse as plants, arachnids, insects, birds and mammals that live in urbanized areas are developing changes in their morphology (Yeh 2004; Badyaev et al. 2008), physiology (Hutton and McGraw 2016), behavior (Dominoni et al. 2014; Shannon et al. 2016) and/or genetics (Hopkins et al. 2018; Mueller et al. 2018).

Why to study movements in urban environments?

In the last centuries the expansion of humans and the consequent loss of natural habitat has forced to most species to live in fragmented and isolated territories (Fahrig 2005; Tremblay and Clair 2011). This has been associated with a growing interest in studies related to animal's movements in altered landscapes, which have been facilitated by the development of tracking devices and the growth of long term monitoring programs (Fisher and Davis 2011). Urbanization is included among the extreme forms of land-use alteration, and the landscape structure and resource availability for wildlife species change substantially along the natural–urban gradient (Faeth et al.2005; Shochat et al.2010). Indeed, urbanization represents an extreme process that may constraint or directly impedes the movements of species, especially of those with low movement capabilities (Prange et al. 2004; Markovchick-Nicholls et al. 2008; Roth and Vetter 2008). This situation can have demographic and genetic consequences, such as a rapid genetic differentiation, genetic drift and inbreeding, and bottleneck effects (Nöel and Lapointe 2010; Björklund et al. 2009; Munshi-South and Nagy 2014; Lourenço et al. 2017). However, in some occasions even wildlife with greater movement capability cope with the growing humanization of the environment by reducing their movements, due to the unavailability of suitable habitat, as confirmed in terrestrial mammals (Tucker et al. 2018), or by the high predictability of subsidized resources, that make unnecessary longer movements and the use of wide territories (Oro et al. 2013; Šálek et al. 2015).

From the different aspects related with the movements that can be studied in urban animals, one of them is the dispersal, the movement of individuals from their birth territory to their first breeding territory (natal dispersal), and the movement from one breeding territory to another in subsequent breeding seasons (breeding dispersal) (Greenwood and Harvey 1982). This trait that can play an important role for individual fitness (Forero et al. 2002; Nevoux et al. 2013) but also can affect the gene flow, the genetic structure and the demographic dynamics of populations (Clobert et al. 2001; Bowler and Benton 2005). Studying dispersal is especially difficult because of its inherent difficulties, and despite of its importance, it has been studied to a lesser

extent than others aspects of the animal ecology (Baguette and Van Dyck 2007; Penteriani and Delgado 2010). Growing evidences confirm that dispersal is a highly plastic trait that responds to factors such as the fragmentation of the natural habitats, the resource availability and/or the population density (Coulon et al. 2010). Moreover, a recent hypothesis named "matching habitat choice" suggests that individuals would tend to occupy different habitats according to their phenotype (Benard and McCauley 2008; Edelaar and Bolnick 2012). Thus, different authors have highlighted that the heterogeneity among individuals and populations regarding their dispersal movements could help to explain colonization processes and the expansion of certain species in new habitats, including cities (Fraser et al 2001; Rehage and Sih 2004). Recent studies support this hypothesis, for example Hanski et al. (2004) and Duckworth and Badyaev (2007) have shown that the phenotypic composition of recently established colonizing populations differs from those of the original population in dispersal traits.

Nonetheless, it is striking to note the few research efforts devoted to understand the dispersal strategies showed by species inhabiting cities (LaPoint et al. 2015; Marzluff 2016). As explained previously, the urbanization supposes a great transformation of the territory, and the species that colonize and thrive in metropolitan areas are subjected to strong selective pressures that can influence their dispersal decisions. Under these circumstances, individuals can disperse in two ways: 1) they may tend to disperse less distance o even remain in the same territory because the own structure of cities, together with the human activities, may limit the movements between suitable patches (Etter et al. 2002); or 2) individuals may show a greater tendency to disperse by intrinsic phenotypic traits or forced by the low availability of suitable patches, which would favor both the initial colonization and the subsequent expansion in such habitat (Møller 2009).

In summary, a wide understanding of the factors that influence dispersal decisions and the distance covered in dispersal movements could help to gain a better understanding of the dynamics of urban and rural populations, as well as the colonization process itself.

The study model

Birds seem to be a suitable study model to study dispersal in urbanized environments, because: this group is widely distributed in cities worldwide (Aronson et al. 2014); there is a reasonable knowledge about avian dispersal (Paradis et al. 1998); and a great number of studies have focused on birds and cities since long ago (Chace and Walsh 2006). Furthermore, dispersal strategies of birds in urban environments remain largely unknown to the date, offering a challenging field to explore in following years.

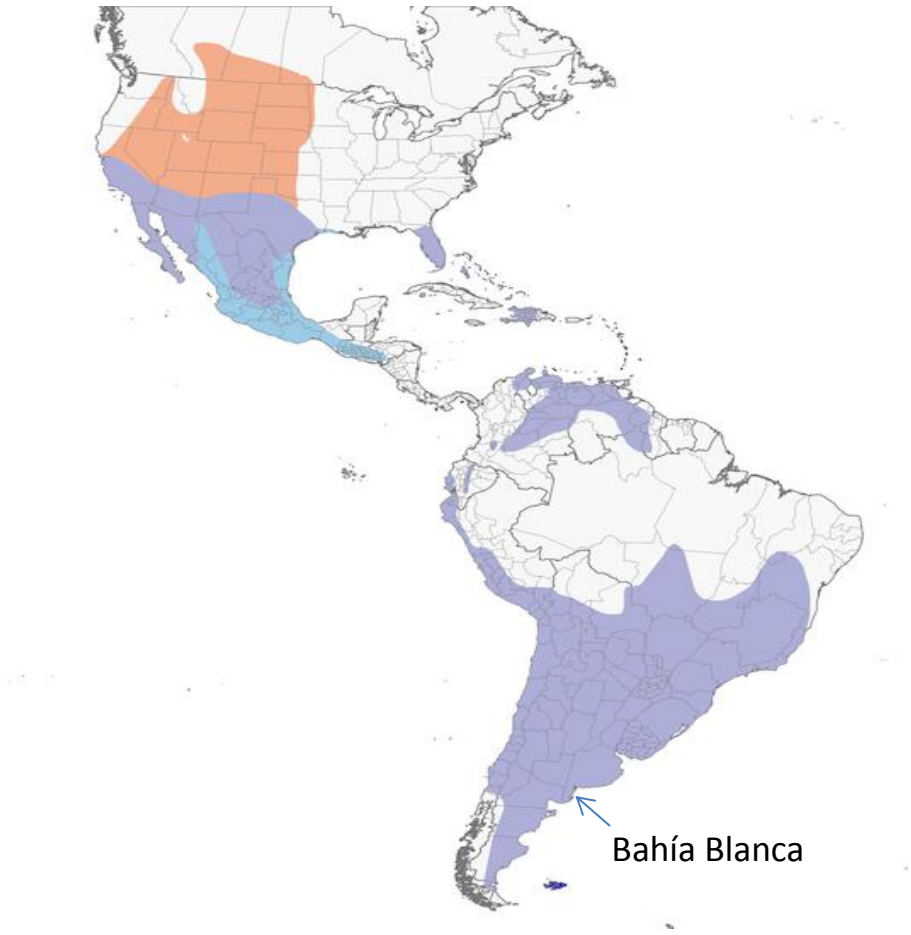
The model species selected for this thesis is the burrowing owl (*Athene cunicularia*) (Fig 1A), a small raptor distributed from Canada to southern Chile and Argentina, with populations also in the Caribbean Islands (Del Hoyo et al. 1999; Poulin et al. 2011;Fig 2). The burrowing owl is an underground nesting bird (Fig 1B) that mainly inhabit shortgrass plains, arid zones, sand dunes, transformed lands dedicated to agriculture and livestock, and urbanized areas (Millsap 2000; Conway et al. 2006; Cavalli et al. 2016; Rebolo- Ifrán et al. 2017). Burrowing owls are active both in the day and the night, hunting a great variety of preys in the ground (Cavalli et al. 2014). The burrowing owl is a medium-short lived species, with a mean life expectancy of 1.3–2.9 years (Carrete and Tella 2013). They start to breed in its first breeding season in which they become adults. Their mean productivity is typically 1.5 – 2.5 fledglings per nest, but the more successful pairs are able to raise 6 chicks (Conway et al. 2006; Griebel et al. 2007; Rebolo- Ifrán et al. 2017). Adults are monogamous and territorials (Rodriguez-Martínez et al. 2014), remaining perched close to the entrance of their burrows most of the time. The unique existent study measuring adult movements indicate that territorial adults have small home-ranges and focus their activity in the surroundings of their territories (Mrykalo et al. 2007).

Figure 1. A) Adult burrowing owl perched close to the nest. B) Typical burrow of burrowing owl decorated with diverse materials.

The study area comprises the city of Bahía Blanca and its surrounding rural areas. Bahía Blanca (38°43'S 62°16'W; Buenos Aires, Argentina; Fig 2) was founded in the first half of the 19th century, being a small settlement until a few decades ago, when the expansion of the city has led to a current population size of almost 300,000 inhabitants. The city is located in a flat landscape, the semi-arid Pampas, a large area dominated by natural grasslands mostly dedicated to low-intensive cereal crops and wide-ranging livestock, with interspersed patches of xerophytic forests and scrublands (Carrete and Tella 2011; Rodriguez-Martínez et al. 2014).

In the city burrowing owls breed in residential areas where they excavate their burrows in spaces between buildings, in the golf course and the cemetery, as well as in roundabouts, avenues, private gardens and public parks, but always in direct contact with the neighbors and with the daily activity of the city (Rodriguez- Martínez et al. 2014). On the contrary, rural burrowing owls breed in natural grasslands and pastures with a few unpaved roads and scarce human presence, mainly devoted to human activities like livestock farming and cereal crops (Carrete and Tella 2010). In these habitats some individuals excavate their nests while others occupy the burrows excavated by the Argentine plains vizcacha (*Lagostomus maximus) (*Rebolo-Ifrán et al. 2017), hence the Spanish name of this small raptor: "lechucita de las vizcacheras".

Figure 2. Distribution range of the Burrowing owl. The color red represents the breeding area for the migrants, and the blue area represents the winter areas. The violet color represents the areas inhabited for year-round residents. Bahía Blanca is the study area of this thesis.



In order to study dispersal, is essential to collect data at individual and population level through long-term studies (Paradis et al. 1998; Camacho et al. 2019). The recent expansion of Bahía Blanca and the subsequent colonization of this city by the burrowing owl make this scenario suitable to develop research programs. Furthermore, this small raptor seems a suitable study model, given that they show diurnal activity, usually remain near to their territories, their nests are easily detectable, and by the high number of breeding territories located in the city and in their adjacent rural area (Rodriguez-Martínez et al 2014; Rebolo- Ifrán et al. 2017). Thus, a monitoring program of the burrowing owl population of Bahía Blanca started in 2006 and still remains active. This represents one of the few cases with such effort

devoted to monitoring a single species in urban environments from a multidisciplinary approach. During these years, different group members have conducted fieldwork each breeding season monitoring the active nests, ringing chicks and adults and assessing the reproductive success. This monitoring program has been complemented with parallel experiments focused in the behavior, genetic, diet and physiology of burrowing owls living in both the urban and the rural area. Results from this long-term study include relevant findings on how the individual susceptibility to human presence influences the distribution of burrowing owls between urban and rural habitats, in a way that urban colonizers are tame individuals while those rural have a major variety of responses to human presence, including both shy and bold individuals (Carrete and Tella 2010; Carrete and Tella 2011; Carrete and Tella 2013). Furthermore, more studies focused in demographic parameters show that individuals inhabiting the city obtain higher reproductive success and have few predatory pressure, hence the higher breeding densities observed in this habitat (Rebolo-Ifrán et al. 2015; Rebolo-Ifrán et al. 2017). Finally, now we know through genetic analysis that the burrowing owl maintains their monogamy breeding behavior (Rodriguez-Martínez et al. 2014).

Thesis hypothesis and chapters

My thesis focuses on the dispersal of the burrowing owl in landscapes with a different degree of anthropization: the city of Bahía Blanca and its rural surroundings. During the long-term monitoring conducted in this species and study area various dispersal strategies have been observed: philopatric adult burrowing owls that remain within their breeding territory over years; young individuals that remain in their natal territory (sometimes cooperating in reproductive tasks with other adults) and; individuals dispersing different distances from their natal or breeding territory.

Gaining knowledge about the causes and consequences of these coexisting dispersal strategies could improve the general understanding of the processes governing its recent urban colonization. Furthermore, this research can provide novel information about how this small raptor thrives in the city, and also explain the factors influencing

their success in such humanized habitat. In addition to this, I can explore whether certain dispersal traits differ between individuals living in the city and the ones from original rural areas, and the potential influence of dispersal processes in the demographic dynamics in this spatially structured population.

The main hypothesis of this thesis is that dispersal is not random, and birds inhabiting habitats with different ecological characteristics as urban and rural landscapes may present differences. Individuals may disperse according to their phenotypes, although their settlement decisions could be also influenced by heterogeneous selective pressures, leading even to the appearance of atypical breeding systems. Furthermore, different dispersal strategies could have different consequences in term of fitness, which could contribute to explain the species demographic and spatial dynamics.

Consequently, the first aim of this thesis is to understand the influence of individual characteristics (behavior, sex and age) and environmental factors (quality of birth and breeding zones, predation pressure and habitat type) on dispersal decisions. Then, the second aim of this thesis is to evaluate whether dispersal decisions influence the main fitness components: the reproductive and survival parameters.

In **chapter 1** I study the factors and consequences of **natal dispersal** decisions in burrowing owls born in urban and rural territories. Given that the urban population is composed mainly by bolder individuals and the rural by individuals with different degree of fear of humans (Carrete and Tella 2017), I consider that if natal dispersal is related to personality traits and environmental cues the strategy adopted may differ between individuals and habitats. To explore this I determine how the type of habitat and social factors related to the environment where the individuals born, in addition to individual traits (sex and behavior) determine natal dispersal distances. Furthermore, I evaluate whether the natal dispersal decisions of burrowing owls have effects in the reproductive success of the individuals (both in the first breeding attempt but also during the lifetime) and in their future survival.

In **chapter 2** I examine the existence of **cooperative breeding** strategies. First, the identity of the adults forming cooperative breeding system is assessed using genetic data and through continuous monitoring of marked individuals. Then, I study the influence of social factors linked to the habitat quality, such as the conspecific density and productivity in the area, together with the habitat type (urban vs. rural) on the probability to develop cooperative breeding systems. Finally, I evaluate the potential consequences of different breeding systems (biparental breeding vs. multiple cooperative breeding) in the antipredator behavior of the adults, the reproductive output (breeding success and productivity) and the survival of the offspring raised.

In **chapter 3**, I explore the factors responsible of **breeding dispersal** decisions of burrowing owls living in urban and rural areas. In this case I first analyze the factors that influence site fidelity (individuals that remain in the same nest), and only for dispersers I evaluate the drivers that contribute to move longer or shorter distances. Having in mind the intrinsic differences of each type of habitat and the behavioral differences between rural and urban individuals, I consider that some individuals may be more prone to disperse, showing differences in their site fidelity and dispersal distances. Here I assess the importance of age, sex, and behaviour, conspecific density around breeding territories, as well as the previous experiences of breeders related with predation events and reproductive success on dispersal and fidelity decisions. Finally, I evaluate the possible influence of breeding dispersal decisions in survival.

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II| Chapters

Chapter 1

"Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls."

Content of this chapter has been submitted to PLOS ONE as:

Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls.

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Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls.

Abstract

There is a growing need to understand how species respond to habitat changes and the potential key role played by natal dispersal in population dynamics, structure and gene flow. However, few studies have explored differences in this process between conspecifics living in natural habitats and those inhabiting landscapes highly transformed by humans, such as cities. Here, we investigate how individual traits and social characteristics can influence the natal dispersal decisions of burrowing owls (*Athene cunicularia)* living in urban and rural areas, as well as the consequences in terms of reproductive success and apparent survival. We found limited dispersal movements among individuals, with differences between urban and rural birds (i.e., the former covering shorter distances than the latter), maybe because of the higher conspecific density of urban compared to rural areas. Moreover, we found that urban and rural females as well as bold individuals (i.e., individuals with shorter flight initiation distance) exhibited longer dispersal distances than their counterparts. These dispersal decisions have effects on individual fitness. Individuals traveling longer distances increased their reproductive prospects (productivity during the first breeding attempt, and lifetime productivity). However, the apparent survival of females decreased when they dispersed farther from their natal territory. Although further research is needed to properly understand the ecological and evolutionary consequences of dispersal patterns in transformed habitats, our results provide information about the drivers and the consequences of the restricted natal movements of this species, which may explain its population structuring through restricted gene flow between and within urban and rural areas.

Introduction

Natal dispersal, defined as the movement of individuals from their birthplace to their first breeding area (Greenwood and Harvey 1982) may influence the future survival, fecundity, and lifetime fitness of individuals (Forero et al. 2002; Doligez and Pärt 2008; Serrano and Tella 2012), playing an important role in the evolution, persistence and spread of populations and species (Skellam 1951; Kokko and López-Sepulcre 2006; Jongejans et al. 2008; Baguette et al. 2013; Kubisch et al.2014; Canestrelli et al. 2016; Bonte and Dairel 2017). Thus, a large number of studies have investigated the factors driving natal dispersal decisions, in particular the importance of social and environmental clues [e.g. conspecific density and habitat characteristics (Doligez et al. 2004; Garant et al. 2005), previous experience (Davis and Stamps 2004)] and phenotypic attributes, including personality (Fraser et al. 2001; Bize et al. 2017), structural size (Camacho et al. 2013; Camacho et al. 2015), body mass (Barbraud et al. 2003; Garant et al. 2005) and sex (Trochet et al. 2016), among others (reviewed by Clobert et al. 2009). All of these factors can interact in complex and subtle ways, varying across the spatial range of a species, such that natal dispersal decisions, as well as their conditioning, can differ among species but also among populations of the same species (Clobert et al. 2009). Therefore, studies comparing the dispersal patterns of conspecifics inhabiting areas with contrasting characteristics and subjected to different selection regimes are important to better understand the dynamic nature of dispersal as well as how drivers of global change affect the fate of animal populations.

Urbanization is the most drastic and persistent alteration of a landscape, creating new habitats starkly different from the natural habitats it replaces (Grimm et al. 2008). Currently, urbanization is occurring globally at an unprecedented rate, with predictions that, by 2050, approximately 60% of the world's human population will be living in urbanized landscapes (United Nations 2007). Although urbanization leads to an overall loss of biodiversity (the so-called 'biotic homogenization process: McKinney and

Lockwood 1999; McKinney 2006; Sol et al. 2014), some species seem to prosper in these environments (Luna et al. 2018). Among birds, for example, nearly 20% of the roughly 10,000 described species can be found in cities (Aronson et al. 2014). Thus, understanding the factors that allow them to persist within these landscapes as well as the consequences for their population dynamics and structure is as important as identifying the drivers of species loss. A common finding of studies exploring traits that allow individuals to live in urban environments is that urban birds are less fearful of humans (bolder) than their rural counterparts, such that urban colonization may be driven by tame individuals from species with high interindividual variability in fear of humans crossing the disturbance frontier (Carrete and Tella 2010; Møller 2010; Carrete and Tella 2011; Rebolo-Ifrán et al. 2015; Carrete and Tella 2017; Sprau and Dingemanse 2017). Fear of humans, measured as the distance at which an individual flees in response to an approaching person (also called flight initiation distance, hereafter FID), is repeatable throughout the adult lifespan (Carrete and Tella 2013; Bubac et al. 2018), heritable (Carrete et al. 2016), and correlates with other behaviors such as exploration and antipredatory response (Carrete and Tella 2017). Thus, it can be considered a personality trait (Luna et al. 2019). Another common pattern found in the literature is that urbanization leads to a reduction in predators (Díaz et al. 2013; Rebolo-Ifrán et al. 2017), such that species able to colonize urbanized habitats can show larger densities or abundances than their rural counterparts (Møller et al. 2012; Stracey and Robinson 2012; Rodriguez- Martínez et al. 2014; Tella et al. 2014). These changes in individual behaviors or personalities, conspecific density and predation pressure can have profound effects on the demographic parameters of individuals (Rebolo-Ifrán et al. 2015), including their dispersal decisions (Luna et al. 2019). There is a growing literature showing how the dispersal patterns of some species change in response to local conditions and depending on the phenotypic characteristics of the individuals present in a particular population (Kokko and López-Sepulcre 2006; Clobert et al. 2009). Despite this, there are no studies exploring whether urban individuals show different natal dispersal movements than their rural counterparts.

Here, we use the burrowing owl (Athene cunicularia) as a study model to assess the role played by individual characteristics (i.e., sex, and personality), and the environment where an individual was born (i.e., the breeding density and productivity of conspecifics) on the natal dispersal distances of urban and rural individuals. We predict that if natal dispersal is related to individual personality, bold and shy individuals (i.e., those with short and large FID, respectively) will breed at different distances from the sites where they were born. Some studies show that boldness is associated with dispersal tendency (Fraser et al. 2001; Dingemanse et al. 2003; Cote et al. 2010; Duckworth and Badyaev 2007) and thus, urban birds should have longer natal dispersal distances than rural ones. However, our previous work has indicated that the breeding dispersal propensity of burrowing owls is personality-dependent among rural but not urban individuals, with shy birds moving further than bold ones but only in the rural habitat (Luna et al. 2019). Moreover, as avian females usually move greater distances during dispersal than males (Clarke et al. 1997; Dale 2001), we expect to find this general pattern among all urban and rural individuals. Social features such as conspecific density and productivity can be used by individuals as indicators of habitat quality, such that dispersers would prefer to move to high-density and high-productivity areas (Boulinier et al. 2002; Serrano et al. 2003; Payo-Payo et al. 2018). However, young individuals born in very dense areas could also disperse to low-density areas to avoid intraspecific competition (Matthysen et al. 2005; Rodrigues et al. 2014). In our study model, predation, the main determinant of individual fitness (Rebolo-Ifrán et al. 2015; Rebolo-Ifrán et al. 2017), is highly unpredictable; thus, conspecific presence and productivity can be used as indicative clues of predation risk. We expect that individuals born in areas with low conspecific density and/or productivity move to other areas of higher quality (i.e., high conspecific density and/or productivity). As urban areas have fewer predators than rural ones (Rebolo-Ifrán et al. 2017), this pattern is expected to be more pronounced among birds living in more natural areas. Finally, we evaluated posterior survival and reproductive output. We predict that due to the risk associated with moving to areas far from their natal sites, where individuals are not familiar with the habitat and predation is difficult to assess, birds moving

greater distances should have lower reproductive output and survival than those staying close to their natal areas (Serrano and Tella 2012).

Material and methods

Study system and field procedures

The study area covers approximately 5,400 km2 of natural grasslands, pastures and cereal crops, surrounding the city of Bahía Blanca, Argentina (Carrete and Tella 2010; Carrete and Tella 2013). We surveyed burrowing owls from 2006 to 2018, monitoring ca. 2500 and ca. 3200 urban and rural nests, respectively. Urban nests were located in private and public gardens, vacant lots among houses, curbs of the streets, roundabouts, and large avenues, in contact with the intense daily activity derived from cities. Rural nests, on the contrary, were located in large extensions of natural or semi-natural grasslands, with very low human presence. It is worth noting that the city is immediately surrounded by large areas of pastures, and there is no obstacle precluding the movement of individuals between urban and rural areas. Moreover, as these owls are able to excavate their own burrows, their distribution is not constrained by the availability of nesting structures.

During the breeding period (from November to early February), all known breeding sites and areas of suitable habitat for the species were regularly visited, and active nests were georeferenced using a portable GPS. Chicks were captured at their natal nests using bow nets and ribbon carpets, and marked with plastic coloured and numbered rings readable at a distance. Resightings of marked birds were done annually during the breeding period, throughout the study area (Rebolo- Ifrán et al. 2017). At the end of every breeding season (except in 2018), we recorded the productivity of each nest as the number of young that reached fledging age.

Natal dispersal distance was measured as the straight line between an individual's nest site and its first breeding nest. Individuals that were not observed in their first but in their second breeding season were included in our analyses, using as natal dispersal distance the straight line between their natal site and their second breeding nest. In

these cases, we assumed that natal dispersal distances were larger than the short breeding dispersal distances recorded for the species (Luna et al. 2019), such that the breeding location at the second nest would not be far from the first breeding point. However, we cannot discard the possibility that those birds were actually breeding for their first time at 2 years of age, and that this dispersal distance corresponds to their natal dispersal.

We sexed adult birds based on plumage pattern and coloration (Carrete and Tella, 2013) and, when needed, by molecular procedures (Rodriguez- Martínez et al. 2014). FID was measured using the standard procedure of walking toward undisturbed individuals perched close to their nests during the day and recording the distance at which the bird flew away (Carrete et al. 2016). Both single and average values of FID were used, given the high repeatability of this behavior ($r = 0.91$; Carrete and Tella 2013). Conspecific density was calculated using an annual aggregation index for each breeding pair, obtained as their relative position within the spatial distribution of all breeding pairs (Carrete et al. 2006). This index reflects conspecific density and was obtained using the GPS location of all breeding pairs as $Si = \Sigma \exp(-dij)$ (with $i \neq j$), where dij was the linear distance between pairs i and j. We also estimated the productivity of the breeding pairs in the surroundings of each breeding site using a modification of this aggregation index, where the distance of each breeding pair was weighted by its productivity. Conspecific productivity was then obtained as the residual of this last variable against the aggregation index calculated previously.

Statistical approach

We used Generalized Linear Mixed Models (GLMM) to assess the effects of individual traits (sex and personality, measured as FID), and social variables (conspecific density and productivity in the natal area) on the natal dispersal distances (log-transformed, identity link function, normal error distribution) of urban and rural burrowing owls.

Due to the low proportion of birds that bred for the first time in their natal nests (philopatric individuals), dispersal distance was modelled as a continuous variable ranging from 0 to the maximum distance observed. Models were built using a different combination of variables in interaction with habitat (urban or rural) but including alternatively only one descriptor of the social environment (conspecific density or productivity) due to their slight, but significant, correlation (Spearman correlation: rho=0.41, $p<0.0001$). All models included the year as a random variable.

We then compared the social environment of individuals (conspecific density and productivity; identity link functions, normal error distributions) between natal and dispersal sites. Due to differences in conspecific density and productivity between rural and urban areas, we included the habitat of recruitment as a factor in the models. We tested whether these differences were related to the individuals' dispersal distances, again considering potential habitat differences. All models included the year as a random variable to control for inter-annual differences.

Next, we assessed the effect of dispersal distance on immediate (the first breeding event) and lifetime productivity of individuals (log link functions, negative binomial error distributions). To calculate lifetime productivity (i.e., fledglings raised by an individual during its lifetime), we only considered individuals with known reproductive output for every year during their reproductive careers and not seen during at least 2 years prior to the end of this study (until 2016), which had a very high probability of being dead (probability of not resighting an alive individual over 2 years at least once was 0.005 for males and 0.033 for females). Models included the dispersal distance of individuals, the habitat where the bird bred, and its sex. Models obtained for lifetime

productivity also included, for each year (random term), the age of each bird (covariate) and its identity (random term) to control for potential improvements along years and pseudoreplication (Serrano and Tella 2012). We also considered potential habitat and sexual differences by including the interaction between sex and dispersal distance and between habitat and dispersal distance in models.

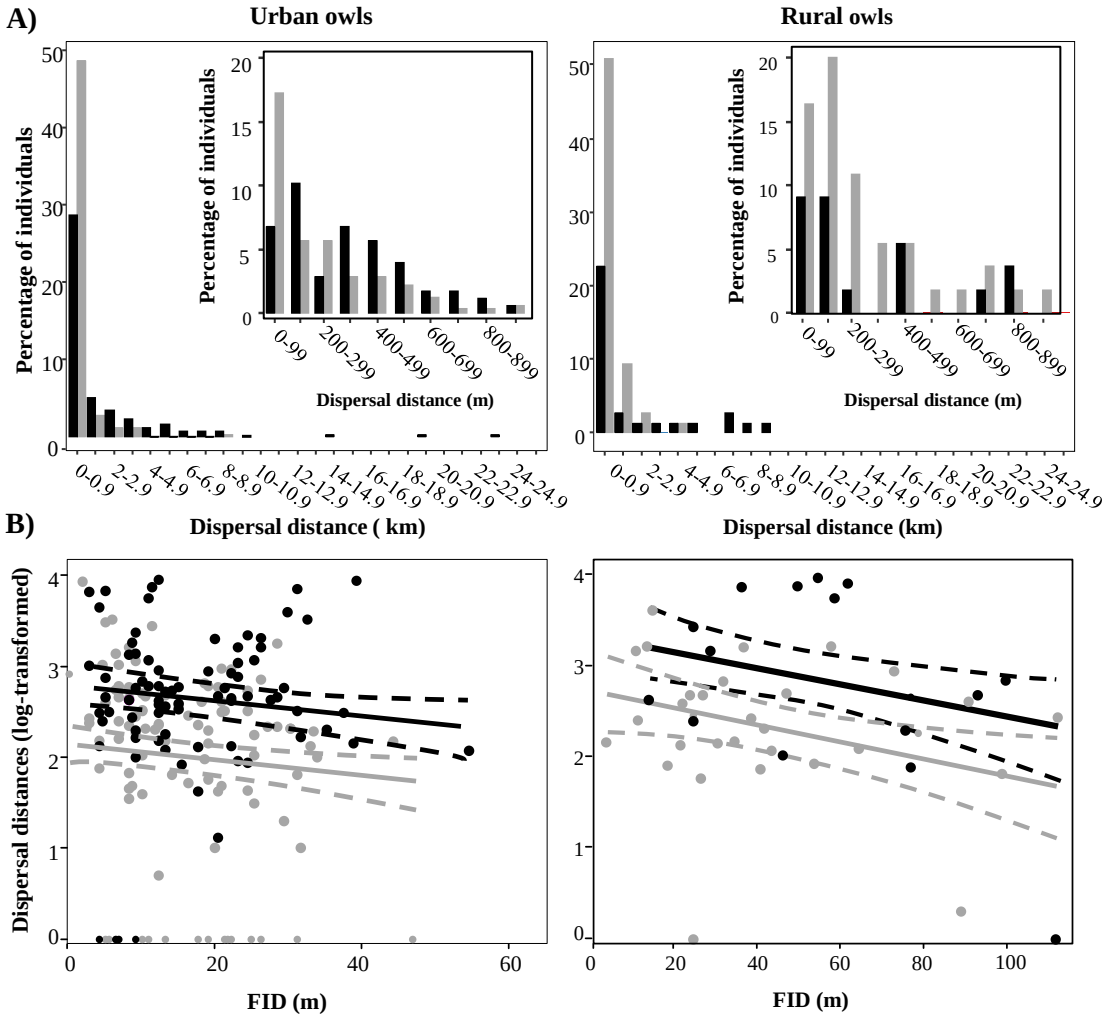
Model selection was performed using the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Models within 2 AICc units of the best one were considered as alternatives and used to perform model averaging (MuMIn package,Barton 2017). All continuous variables were centered before modelling to properly estimate their main effects regardless of whether we included the interaction (Grueber et al. 2011). We considered that a given effect received no, weak or strong statistical support when the 95% confidence interval (CI) strongly overlapped with zero, barely overlapped with zero, or did not overlap with zero, respectively. Finally, we calculated the coefficient of determination, R2, as a measure of the variance explained by a model (Nakagawa and Schielzeth 2013). Statistical analyses were conducted in R 3.1.2 (R Development Core Team 2008) (using the package “lme4”, Bates et al. 2015).

We modelled apparent survival following basic capture–mark–recapture methods for open populations, in which return rates were corrected for recapture (p) probabilities (Lebreton et al. 1992). For this purpose, we created encounter histories for every marked individual with known natal dispersal distances. We evaluated if adult apparent survival was related to natal dispersal distance (log transformed) by including it as an individual covariate while habitat (rural and urban) and sex were considered as factors. We first tested the effects of time, habitat and sex on recapture and, once the best structure for this parameter was selected, we modelled survival. Models differing by < 2 AICc points were considered equivalent (Burnham and Anderson 2002). We tested the goodness-of-fit of our global model using the program U-CARE (Choquet et al. 2009a). Models were implemented in the program E-SURGE 2.1.4 (Choquet et al. 2009b).

Results

During the study period, we marked 830 urban and 566 rural burrowing owls with PVC rings, and were able to record 321 natal dispersal events in 75 rural (48 males and 27 females) and 246 urban (129 males and 117 females) birds. However, as FID was not measured for all individuals, our dataset was reduced to 224 individuals, 85% of which were resighted during their first breeding. Although some individuals moved more than 10km, median dispersal distance was much shorter (322m), and most birds bred for the first time close to their natal areas (percentage of individuals remaining within 1 km of their natal sites: 75%; Figure 1A) and in the same habitat of birth (96% of dispersions were within the same habitat type). Movements between habitats were rare (10 individuals out of 224), and mainly from urban to rural areas (6 movements from urban to rural areas vs 3 movements from rural to urban ones).

Figure 1. A) Natal dispersal distances of urban and rural burrowing owls *Athene cunicularia* (males: grey bars; females: black bars). The inserted figure shows a detailed distribution of dispersal distances lower than 1km. B) Relationship between natal dispersal distances (log-transformed) and individual personality (measured as FID, flight initiation distance). Lines show the tendency observed for males (grey line) and females (black line). Dashed lines represent the 95% confidence interval. Dots are raw data (males: grey dots, females: black dots).



Correlates of natal dispersal

Sex, individual personality and habitat were the most important variables to explain interindividual differences in natal dispersal distances (Table 1). Urban birds dispersed over shorter distances than rural ones, with females moving farther than males in both habitat types. Moreover, individuals with shorter FID dispersed at greater distances than their counterparts, regardless of their sex or the habitat where they were born (Figure 1B). Although social variables were weakly related to dispersal distances, individuals born in areas with low conspecific density tended to cover greater distances than those born in high-density areas (Table 1). Importantly, when habitat was removed from the analysis, conspecific density received stronger support as a predictor of dispersal distances, with individuals born in high-density areas dispersing less than those born in more isolated sites (Table 1). This change in the result suggests that, besides the higher conspecific density recorded in the surroundings of urban compared to rural sites (estimate: 13.16, 95% CI: 10.99 - 15.33), there are other traits associated with urban sites that may be affecting natal dispersal decisions. Finally, we found no differences in conspecific density or productivity between natal and dispersal areas in both habitat types (conspecific density: estimate: 2.44, 95% confidence interval: -5.58 - 1.35; conspecific productivity: estimate: 0.65, 95% confidence interval: -0.29 - 1.59). However, individuals dispersing farther settled in areas more similar in terms of conspecific densities than those staying close to their natal areas (estimate: -1.17, 95% CI: -2.20 - -0.15), a pattern not observed when considering changes in conspecific productivity (estimate: 0.27; 95% CI: -0.77 - 1.32). It is worth noting that similar results were obtained when restricting our dataset to individuals resighted during their first breeding attempt (Table S1).

Table 1. Relative importance of individual's traits (sex and personality, measured as FID), and social variables (conspecific density and productivity in the natal area) on the natal dispersal distances of rural and urban (habitat) burrowing owls Athene cunicularia. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped with zero, barely overlapped with zero (asterisk), or did not overlap with zero (in bold), respectively. Models shown are the first 10 models ranked using their AICc. Variable (*): model averaging performed using the subset of models that did not include habitat. w: Akaike weights.

Model	K	AICc	ΔAICc	w
FID + habitat + sex	6	590.51	0.00	0.25
conspecific density + FID + habitat + sex	7	590.86	0.35	0.21
conspecific productivity + FID + sex + habitat	7	592.53	2.03	0.09
conspecific density + FID + sex (*)	6	592.93	2.42	0.07
conspecific productivity*habitat + FID*habitat + sex*habitat	10	593.07	2.56	0.07
conspecific density + sex (*)	5	593.16	2.65	0.07
habitat + sex	5	593.70	3.19	0.05
sex (*)	4	594.34	3.83	0.04
conspecific density + habitat + sex	6	594.61	4.10	0.03
FID*habitat + sex*habitat	8	594.70	4.20	0.03

Variable	Estimate	2.50%	97.50%
FID	**-0.18**	**-0.34**	**-0.03**
habitat (urban)	**-0.49**	**-0.88**	**-0.09**
sex (female)	**0.63**	**0.40**	**0.87**
conspecific density	-0.10	-0.25	0.05

Variable (*)	Estimate	2.50%	97.50%
FID	**-0.10**	**-0.23**	**0.03***
sex (female)	**0.59**	**0.35**	**0.83**
conspecific density	-0.14	-0.28	0.00

Correlates of natal dispersal distances on productivity and survival

Birds breeding for their first time in rural areas were less productive than those inhabiting urban ones (Table 2). However, when they dispersed farther from their natal areas, they raised more chicks during their first breeding attempt than those staying nearby, a relationship that was absent among urban individuals. Besides, females dispersing at larger distances of their natal areas also increased their productivity in the first breeding event. When considering the lifetime productivity of individuals (data available for 144 individuals), we found that all birds, urban and rural, tended to increase productivity with age and when disperse at greater natal distances (Table 2). Results remained consistent when we repeated models using only individuals resighted during their first breeding attempt (Table S2).

Table 2. Relationship between natal dispersal distances and productivity during the first breeding attempt, and lifetime productivity of rural and urban (habitat) burrowing owls *Athene cunicularia*. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped with zero, barely overlapped with zero (asterisk), or did not overlap with zero (in bold), respectively. All models were run including year as a random term; models for lifetime productivity also included individual as a random term. Models shown are the first 10 models ranked using their AICc. w: Akaike weights

Productivity during the first breeding attempt

Model	k	AICc	ΔAICc	w	Variables	Estimate	2.50%	97.50%
sex + dispersal distance*habitat	7	1372.93	0.00	0.42	dispersal distance	-0.27	-0.82	0.28
dispersal distance*sex + habitat	7	1374.79	1.86	0.17	**sex (females)**	**0.50**	**0.13**	**0.87**
dispersal distance*sex	6	1374.90	1.96	0.16	habitat (rural)	-0.36	-0.76	0.04
sex	4	1376.48	3.55	0.07	dispersal distance*sex (females)	**0.62**	**0.05**	**1.19**
sex + habitat	5	1376.54	3.61	0.07	dispersal distance*habitat (rural)	**0.42**	**0.11**	**0.72**
dispersal distance*habitat	6	1377.89	4.96	0.04				
sex + dispersal distance + habitat	6	1377.99	5.06	0.03				
sex + dispersal distance	5	1378.24	5.31	0.03				
dispersal distance + habitat	5	1382.84	9.91	0.00				
dispersal distance	4	1383.60	10.67	0.00				

Lifetime productivity

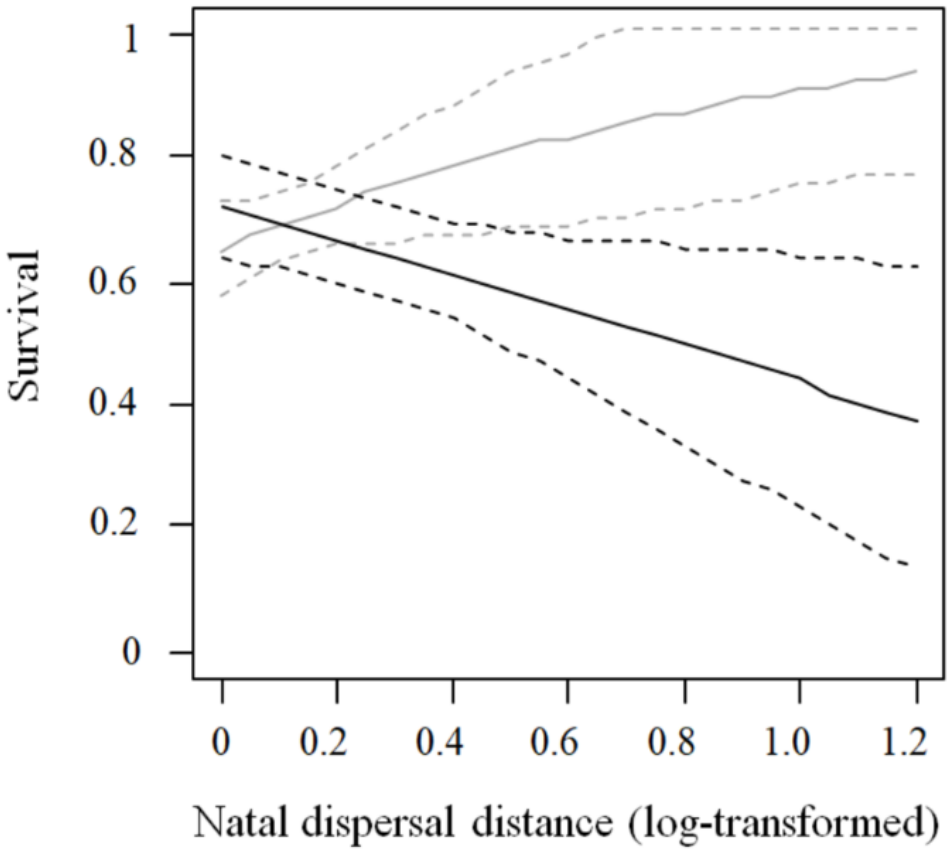
Model	k	AICc	ΔAICc	weight	Variables	Estimate	2.50%	97.50%
sex + age	5	1239.58	0.00	0.20	**sex (female)**	**0.27**	**0.10**	**0.45**
sex + age	5	1239.58	0.00	0.20	**age**	**0.08**	**0.03**	**0.14**
sex + age + habitat	6	1240.69	1.11	0.11	habitat (urban)	0.11	-0.11	0.34
sex + age + habitat	6	1240.69	1.11	0.11	dispersal distance	0.02	-0.06	0.11
sex + age + dispersal distance	6	1241.34	1.76	0.08				
sex + age + dispersal distance	6	1241.34	1.76	0.08				
sex + age + dispersal distance + habitat	7	1242.15	2.57	0.05				
sex + age + dispersal distance + habitat	7	1242.15	2.57	0.05				
sex + age + dispersal distance*habitat	8	1242.48	2.90	0.05				
sex + age + dispersal distance*habitat	8	1242.48	2.90	0.05				

We estimated the effect of dispersal distances on future apparent survival probabilities using encounter histories of 248 individuals (1411 resightings). The overall goodness-of-fit test of the model was not statistically significant (χ^2 = 34.34, d.f. = 43, p=0.824). Model selection showed that resighting probabilities were lower for females (estimate: 0.82, 95% CI: 0.72 - 0.90) than for males (estimate: 0.93, 95% CI: 0.86 - 0.96; Table 3). Using this resighting structure, we tested the effect of natal dispersal distances on survival probabilities. The best model supported an interaction between dispersal distance and sex (Table 3), with females dispersing farther reducing their survival prospects compared to females staying closer (beta estimate: -1.21, 95% CI: -2.29 - -0.14). For males, future survival was not correlated with dispersal distances, the estimate of the slope of this variable was not different to 0 (beta estimate: 1.60, 95% CI: -0.30 - 3.50; Figure 2). Habitat was not retained in models as a significant predictor of survival.

Table 3. Model comparison to assess the effects of natal dispersal distances (distance) on immediate survival probabilities of urban and rural (habitat) burrowing owls Athene cunicularia. Smaller AICc values suggest a better fit of the model to data while also penalizing for complexity (k, number of parameters). Models whose AICc values differ from that of the top model by less than two (ΔAICc < 2) are considered as alternative relative to the top model.

Survival model	Resighting model	k	deviance	AICc	ΔAICc
distance*sex	sex	6	735.58	747.73	0.00
constant	sex	3	744.20	750.25	2.51
distance	sex	4	743.24	751.24	3.51
sex	sex	4	743.72	751.80	4.06
habitat	sex	4	744.17	752.25	4.51
distance*habitat	sex	6	740.19	752.35	4.62
distance+sex	sex	5	743.03	753.14	5.41
distance+habitat	sex	5	743.18	753.29	5.55
habitat+sex	sex	5	743.66	753.77	6.03
time	sex	12	729.65	754.24	6.50
time+sex	sex	13	728.62	755.30	7.57
habitat*sex	sex	6	743.57	755.73	7.99
time+habitat	sex	13	729.65	756.33	8.60
time+habitat+sex	sex	14	728.59	757.38	9.65
time*sex	sex	20	722.68	764.29	16.55
time*habitat	sex	21	722.75	766.51	18.78
time*habitat*sex	sex	36	703.86	781.10	33.37
time*habitat*sex	constant	35	707.06	782.01	34.28
time*habitat*sex	habitat+sex	37	703.84	783.39	35.65
time*habitat*sex	habitat	36	707.05	784.29	36.56
time*habitat*sex	habitat*sex	38	703.56	785.42	37.68
time*habitat*sex	time+sex	41	697.32	786.17	38.43
time*habitat*sex	time	40	700.19	786.70	38.96
time*habitat*sex	time+habitat+sex	42	697.31	788.51	40.78
time*habitat*sex	time+habitat	41	700.17	789.02	41.29
time*habitat*sex	time*sex	46	695.13	795.81	48.08
time*habitat*sex	time*habitat	46	697.52	798.21	50.47
time*habitat*sex	time*habitat*sex	57	682.28	809.86	62.13

Figure 2. Relationship between survival probabilities of male (gray lines) and female (black lines) burrowing owls Athene cunicularia. Solid lines represent the general tendency; dashed lines: 95% confidence intervals.



Discussion

Our results show that variability in the natal dispersal distances observed among burrowing owls was mainly explained by the additive effects of sex, personality and habitat. As expected, females moved farther distances than males in both habitat types, while urban birds (both males and females) dispersed over shorter distances compared to rural ones, partly because of the higher conspecific density recorded in urban compared to rural areas. Moreover, bold individuals —those with shorter FID dispersed larger distances than their counterparts, regardless of their sex or the habitat and social environment in which they were born.

Sexual differences in natal dispersal distances are common among vertebrates to prevent mating between close relatives (inbreeding avoidance: Pusey 1987; Szulkin and Sheldon 2008; Lebrige et al. 2010). However, the sex that disperses farther is not always the same and largely depends on the prevailing mating system of the species. In resource-defence mating systems, which is the prevailing system among birds, natal dispersal distances are generally shorter for males because they have to acquire and defend territories and, therefore, they may benefit from remaining near their natal area, where they are most familiar with resources and are probably best able to compete for them (Clarke et al. 1997; Pärt 1995; Piper et al. 2008). In our study species, males, but rarely females, actively defend an area larger than that immediately surrounding the nest burrow from conspecifics, with a more active response toward intruders at distances shorter than 100m (Moulton et al. 2004). This behavioral difference between sexes may underlie the sexual differences observed in the dispersal distances of individuals.

Sex is not the only individual trait affecting dispersal distances among burrowing owls. Previous findings showed that bolder, more asocial, and more active individuals can move greater distances and are more suited to colonizing new areas than shyer, social and less active ones (Fraser et al. 2001; Fogarty et al. 2001; Cote et al. 2010). In

agreement with these results, we found a significant negative relationship between FID and natal dispersal among both urban and rural males and females. After settling in a breeding site, however, these bold individuals are more faithful than shy ones (Luna et al. 2019). This apparent contradiction can be solved when considering the different behaviors correlated with FID. On the one hand, FID is positively correlated with explorative behavior (Carrete and Tella 2017). Thus, bold individuals, which are also more explorative, can search for breeding sites exploring wider areas during their natal displacements than shy owls. When settled, however, bold individuals tend to remain in their breeding sites during consecutive years, even after suffering predation events that may cause their breeding failure (Luna et al. 2019). A frequent finding from a wide range of vertebrate species is that individuals may change breeding sites after a poor breeding performance (Beletsky and Orians 1991; Nager et al. 1996; Forero et al. 1999), or under predation pressures (Greig-Smith 1982; Gavin and Bollinger 1988; Wiklund 1996). However, bolder individuals, which are also more aggressive toward predators (Carrete and Tella 2017) can choose to remain in their breeding site and cope with this important conditioning to take advantage of site familiarity.

Social variables received limited support in our modelling approach when we considered the habitat where individuals were born. However, after removing this factor from models, conspecific density became a strong predictor of dispersal distances, with individuals born in areas with low conspecific density covering greater distances than those born in high density areas. Thus, differences in natal dispersal patterns among urban and rural birds could be partially attributed to differences in conspecific density between habitats. Although high population densities can reduce individual fitness via increased competition for resources or direct interferences between individuals, thus promoting dispersal (Bowler and Benton 2005), our results did not support this hypothesis. Conversely, burrowing owls dispersed at shorter distances when born in high-density areas. Several studies have shown that individuals use information about conspecifics (i.e., their presence, density or breeding performance) to predict habitat quality and thus select whether or not to settle (Danchin et al. 1998; Brown et al. 2000; Serrano et al. 2003; Danchin et al. 2004).

Young burrowing owls recruit into their breeding territories during their first year of life, so they are not able to use conspecific productivity as a proxy of habitat quality. Conversely, they can use conspecific density. Conspecific density can correlate with habitat quality due to the movement of individuals to high-quality patches and/or to the differential mortality of resident conspecifics. In our study species, predation is the main determinant of breeding failure (Rebolo-Ifrán et al. 2017; Luna et al. 2019), so areas with a high density of conspecifics can represent areas where predation risk is rather low.

In vertebrates, current evidence suggests that natal dispersal could be penalized in terms of fitness (Serrano and Tella 2012), although some researches have reported opposite patterns (Lemel et al. 1997; Spear et al. 1998). The low natal dispersal distances observed in our study suggest that moving far from areas where individuals were born is not the preferred strategy for burrowing owls. However, when analyzing the relationships between individual survival and breeding prospects, we found that females and rural individuals dispersing farther from their natal areas raised more chicks during their first breeding attempt than those staying close, a relationship that was absent among urban individuals. Moreover, lifetime productivity tended to increase when both urban and rural individuals dispersed at greater distances from their natal areas. Contrarily, females dispersing farther reduced their survival prospects compared to females staying closer and males. Thus, the reproductive benefits associated with large natal dispersal in females are outweighed by its survival costs (Tarwater et al. 2010; Bonte et al. 2012; Cox and Kesler 2012). This, along with the benefits obtained by males that stay close to natal areas, explain the low dispersal distances observed in the whole population. Although we cannot discard the possibility that the lower survival of females dispersing longer distances arises as a consequence of permanent emigration, the large size our study area (5400km^2) and the intensive monitoring we performed (as shown by the large resighting probability observed for all individuals, independently of their sex and habitat) reduce this likelihood (Serrano and Tella 2012).

In conclusion, we found evidence supporting a role for individual traits (sex and personality) and conspecific density in explaining variability in the natal dispersal patterns of burrowing owls. Although urban areas per se did not affect this demographic parameter, the lower predation risk experienced by urban individuals may favor greater conspecific densities, which actually reduce dispersal propensity. From an evolutionary perspective, and although it is known that very low rates of dispersal among subpopulations are sufficient for the system to behave as a panmictic population (Hoelzel and Dover 1991) rates of dispersal among subpopulations determine the level of gene flow and could, therefore, affect processes such as local adaptation. Thus, the low natal dispersal distances combined with reduced breeding dispersal may be the underlying cause explaining the genetic structure detected among urban and rural populations of burrowing owls at small spatial scales (Mueller et al. 2018). Further research is needed to assess the generalizability of these results to other taxa to properly ascertain the consequences of urbanization in the ecology and evolution of species thriving in anthropogenic areas.

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Chapter 2

“Kinship, ecological determinants and fitness benefits of cooperative breeding in a typically monogamous owl.”

Kinship, ecological determinants and fitness benefits of cooperative breeding in a typically monogamous owl.

Abstract

In some species mature individuals forgo their reproduction to raise the brood of other breeders, generally related to them. These extra adults can contribute genetically to the offspring they care, but its collaboration may be focused only in reproductive related tasks. Sometimes the development of cooperative behavior can have fitness consequences both for the adults involved and the offspring. The burrowing owl is a typically bi-parental species that occasionally form cooperative breeding systems. Using a detailed long term database (approximately 2000 individuals marked and monitoring of more than 5000 nests during 12 years), we evaluate which individuals compose cooperative breeding systems and how spatial and social factor influence their development (conspecific density, productivity and habitat type: urban vs rural). Moreover, we explore whether the presence of helpers influences the brood condition, and whether their contribution improves the reproductive success and/or the survival of the offspring. Our results show that cooperative families are generally composed by two males and one female. This atypical breeding system appears by the delayed dispersal of grown males, which remain one additional year with their parents instead of breed independently. Cooperative breeding strategies are twice more frequent in urban environments, however, the probability of adopting this behavior is especially high in those areas with high density of nests. The body condition of chicks raised by cooperative families is higher, indicating that helpers may increase food provisioning. Reproductive outcome is higher at territories with the presence of helpers. Offspring raised by cooperative breeding systems show a slightly higher future survival than offspring raised by pairs.

Introduction

Cooperative breeding is a reproductive system that arises when more than two adults exhibit parental behavior towards a single brood (Cockburn 2006). It can occur in form of typical polygamy, in which more than one male or female share breeding status, but in some occasions the extra adults involved do not contribute to the genetic pool of the brood that they care (Hatchwell and Komdeur 2000). Kin-selection can explain the appearance of those altruistic individuals (helpers), generally mature individuals that do not reproduce to help other breeders in reproductive tasks (Cockburn 1998). However, especially in colonial and/or authentically social species, cooperative behavior is not strictly restricted to interactions among kin (Heg and van Treuren 1998; Clutton-Brock 2002).

On the contrary, in most cases, the development of cooperative breeding strategies involve kin individuals and appear as a consequence of the delayed dispersal of growing offspring (Koenig et al. 1992). Thus, young individuals can delay their settlement in breeding territories and their own reproduction to assist other individuals to care their brood (Cornwallis 2018; Nelson-Flower et al. 2018). Certain phylogenetic components can predispose to the development of cooperative breeding strategies, being a behavior extended among certain bird families (Arnold and Owens 1998; Hatchwell and Komdeur 2000). This suggests that helping behavior could be evolved in different lineages under particular demographical and environmental contexts, for example in species with high survival, low reproductive output and low dispersal (Arnold and Owens 1998; Jetz and Rubenstein 2011). However, social and environmental factors (for example those linked with the habitat quality) can led to the appearance and maintenance over the time of alternative mating systems by affecting the population density and the spatial distribution of individuals (Hatchwell and Komdeur 2000; Baglione et al. 2002).

Nowadays, urbanization constitutes one of the most important landscape transformations, deeply affecting the spatial distribution of species (McKinney 2006; Grimm et al. 2008). Animals vary in their ability to respond to urbanization, according

to different factors as the susceptibility to humans (Møller 2010; Carrete and Tella 2011). Although the expansion of cities can be related to a loss in habitat quality, human ecosystems also entail benefits for certain species, as predator release and predictable food subsidies (Oro et al. 2013). In some cases, species inhabiting cities even have higher reproductive success and reach higher densities than in their original habitats (Rebolo- Ifrán et al. 2017; Luna et al. 2018). The associated increased population density achieved at urban areas could affect dispersal decisions and breeding systems (Rowe and Weatherhead 2007; Møller 2009; Caballero et al.2016; Biard et al. 2017; Luna et al. 2019). Thus, in highly dense habitats or patches young adults may remain at natal territories acting as helpers instead of dispersing due to the scarcity of high quality empty territories (Kokko and Lundberg 2001; Kokko and Ekman 2002). On the other hand, young individuals may delay dispersal to avoid its associated risks by remaining in high quality natal areas, and may benefit from an increased breeding experience (Hatchwell and Komdeur 2000; Pen and Weissing 2000; Bonte et al. 2012). In fact, cooperative breeding has been generally associated with fitness benefits for both the adults involved and the offspring raised (Richardson et al. 2002; Cockburn et al. 2008; Kingma et al. 2010). First, helpers gain experience in reproductive and/or territorial defense tasks, but also may inherit the natal nest or settle in a close known territory (Cockburn 1998; Dickinson and Hatchwell 2004). Dominant breeders also obtain benefits by sharing the work-rate with the helpers, delaying senescence and enhancing their respective future survival and fecundity (Heinsohn 2004; Meade et al.2010; Hammers et al 2019). In terms of fecundity, the presence of helpers increases the number of offspring or clutches produced -probably favored by higher nestling provisioning and/or defense towards potential predators- (Hatchwell et al. 2004; Valencia et al. 2006). Moreover, the offspring raised in cooperative breeding systems can have better body condition and higher recruitment probabilities (Hatchwell et al. 2004; Brouwer et al. 2012; Preston et al. 2016).

Burrowing owls (*Athene cunicularia*) are typically monogamous and breed in bi-parental systems (Rodriguez- Martínez et al. 2014), but sometimes they form cooperative breeding systems. We developed a continuous monitoring of the breeding

population of Bahía Blanca city and its rural surroundings since 2006, allowing the study of dispersal decisions and breeding systems. Concurrent research has evidenced that breeding densities and productivity are notably higher in the city than in their adjacent rural areas, where predatory pressure drive reproductive parameters and generate spatial differences in productivity and territory aggregation (Rebolo- Ifrán et al. 2017). Dispersal processes of burrowing owls are also affected by habitat characteristics, differing between urban and rural areas, responding to conspecific density and reproductive success, and finally varying among sexes –with males being more prone to remain close to familiar territories (Luna et al. 2019).

This highly detailed information allows studying the extent, composition, causes and future benefits of cooperative breeding strategies in this species. Then, we hypothesized that 1) the extra adults forming cooperative breeding systems may be kin males and the presence of this alternative breeding system may be more probable in highly dense and productive areas; and 2) the additional help occurring in cooperative breeding systems may influence positively in the number of fledglings raised in such territories, and also in their quality and future survival prospects. To address these hypotheses we: 1) we combine genetic with observational data to assess the kinship between the adults participating in cooperative breeding; 2) we evaluate how social related factors (the conspecific density, the productivity in the area and the habitat per se) may drive the development of cooperative breeding; 3) and finally we compare the reproductive output and brood quality in bi-parental and cooperative breeding territories, and the future survival of the offspring raised in both type of breeding systems.

Material and methods

Study species and area

Our study area encompasses 5,400 km^2 of large rural expanses of natural and transformed grasslands around Bahia Blanca city (Buenos Aires, Argentina). Rural owls breed in natural grasslands and pastures dedicated to cattle, where human presence is rare and mostly restricted to some scarce roads and scattered farms (Rebolo-Ifrán et al. 2015). Urban owls, conversely, excavate their own nests in private gardens, public parks, unbuilt spaces among houses, roundabouts, and large avenues, in continuous contact with people and traffic. The city is immediately surrounded by large rural expanses of natural and transformed grasslands, without barriers that may constrain the movements of owls between habitats (Carrete and Tella 2013). Moreover, as owls are able to excavate their own burrows (Machicote et al. 2004) there are no constraints on the availability of potential breeding territories that can limit their dispersal (Rodríguez- Martinez et al. 2014; Luna et al. 2019). However, the short dispersal distance of the species (which is even lower in urban compared to rural areas) combined with differences in individual's personalities (fear of humans) seems to have contributed to the genetic separation of rural and urban populations in the last few decades (Mueller et al. 2018).

From 2006 to 2017, we annually monitored the breeding population of the species in the study area from October to February (austral spring and summer), totalling ca. 2,200 urban and 3,000 rural nests during the whole period. Breeding sites were repeatedly visited to know the identity of the breeding individuals, the type of reproductive units they formed (i.e., breeding pair formed by 2 adults or cooperative unit formed by 3 or more individuals), their breeding success and productivity (i.e. the number of young fledged per breeding attempt), and to capture adults and chicks using bow nets and ribbon carpets. All captured birds were marked by using plastic rings with an individual alphanumeric code and released after measuring (wing length, in millimetres), weighing (in grams) and bleeding (0.1 ml) them. Blood samples were preserved in absolute ethanol and kept at 4ºC until their processing in the laboratory.

Individuals were sexed based on plumage characteristics (Carrete et al. 2013) and, when needed, by molecular procedures (Rodríguez-Martínez et al. 2014).

Delayed dispersal and kinship

We genotyped individuals belonging to 5 complete cooperative families (all adults and chicks) using 17 polymorphic microsatellites previously tested for the species (see Rodriguez-Martínez et al. 2014 for details) to know the relatedness between the adults involved in cooperative breeding systems. DNA was extracted from blood samples using a modification of the silica-based protocol (Ivanova et al. (2006). Then, the loci were amplified by PCR in 2 independent multiplex reactions. For each PCR sample, 1.5 ml of the primers mix (5 ml of each in a final concentration of 2 mM), 3 ml of RNase free water (provided with the QIAGEN Multiplex PCR master mix), 4 ml of template DNA and 6.5 ml of QIAGEN Multiplex PCR master mix were used. The reaction consisted in a 5 min denaturation step at 95ºC, 32 cycles of 30 seconds at 95ºC, 90 seconds at 55ºC and 30 seconds at 72ºC, and ending with a final step of 30 minutes at 60ºC. PCR products were run on 1.5% agarose gels to check for amplification and yield, and then on an ABI3100 DNA analyzer to find DNA sizes. Genotypes were assigned in two ways, manually and automatically, using GeneMapper 3.7 (Applied Biosystems, Foster City, CA), and all electropherograms obtained were independently checked by two experts.

All the microsatellites included in the study were at Hardy-Weinberg and linkage equilibrium (Rodriguez-Martínez et al. 2014). The kinship among the adults was assigned using the program Cervus 3.0.3 (Kalinowski et al. 2007), applying a likelihood-based approach to assign parentage, combined with simulation of parentage analysis to determine the confidence of parentage assignments. We generated 100,000 simulated offspring, assuming 0.7 % sampled parents, 99 % loci typified, an inbreeding rate of 0.06%, and a genotyping error of 0.01 (Rodríguez-Martínez et al. 2014). Previous studies have confirmed genetic monogamy in the burrowing owl (Rodríguez-Martinez et al. 2014), so we complemented the information about the relatedness among adults of cooperative units using information obtained through year by year resights of birds marked as chicks of known parents.

Ecological correlates that drive cooperative breeding

We used Generalized Linear Mixed Models (GLMM) to investigate factors affecting delayed dispersal using the probability of cooperative unit formation as the dependent variable (binomial error distribution, logistic link function). We considered cooperative breeding when more than two adults were observed during the complete breeding season involved in breeding tasks. Otherwise, we considered that the territory was occupied only by a pair. We included the effects of social variables (conspecific density and productivity in the natal area) and habitat (rural vs urban) as explanatory variables, as well as their interactions. "Year" was considered as a random term in models to control for potential interannual differences. Conspecific density was created by an annual aggregation index for every breeding territory, calculated as the relative position of a breeding territory within the spatial distribution of all breeding territories (Carrete et al. 2006). The index was obtained using the GPS location of all breeding territories as $Si = \Sigma\ exp\ (-dij)$ (with $i \neq j$), where dij was the linear distance between pairs i and j. Moreover, we used the conspecific productivity in the surroundings of each breeding territory, calculated as a modification of the same aggregation index, but the distance to each breeding territory was weighted by its reproductive output (number of fledglings raised in that season). Then, conspecific productivity was obtained as the residual of this last variable against the aggregation index calculated previously. Both variables were not correlated (Spearman correlation: rho=0.23, p< 2.2e-16).All covariates were centred before modelling to properly estimate their main effects (Grueber et al 2011). The analyses were done using package lme4 (Bates et al. 2015) in R environment (R Score Team, 2008).

Brood condition and current reproductive output

We explored whether the body condition of chicks is influenced by the breeding system (bi-parental vs. cooperative breeding) and habitat (rural vs. urban) by Linear Mixed Models (LMM). To determine the individual body condition we measured morphometric parameters in captured chicks that were summarized into a body condition index, estimated as the residuals of a log-log regression of body mass on wing length (Schulte-Hostedde et al. 2005; Labocha and Hayes 2012). Considering that some chicks share their natal territory the models included the nest as a random effect to control for non-independence between breeding territories.

We also evaluated potential differences in breeding success and productivity in nests occupied by breeding pairs and cooperative units. First, we tested by GLMM with a binomial error distribution and a logistic link function the effect of the breeding system (biparental vs cooperative breeding) and habitat in the breeding success, as the likelihood of raising at least one chick. Then, we tested the effect of breeding system and habitat on total productivity (number of fledglings raised by nest) by GLMM with a negative binomial error distribution and a logistic link function. All the models performed included the year as a random effect to control for non-independence between years. The analyses were also done with package lme4 (Bates et al. 2015) in R environment (R Score Team 2008).

Future brood survival

Finally, we tested if juvenile and/or adult survival of burrowing owls was related to the natal family structure (bi-parental vs. cooperative breeding) by means of capture-recapture models. To this end we created encounter histories (code 1= observed, code 0= not observed) for every marked chick for which data on natal nest family structure was known (N= 1407 individuals, N= 2060 resightings). Encounter histories were grouped by natal habitat (rural and urban) and family structure (bi-parental vs. cooperative breeding).

Then, we evaluated the potential existence of heterogeneity in survival and or /recapture by assessing the goodness-of-fit tests of the Cormack-Jolly-Seber including

two age classes (φ_{2age*t} p_t) in program U-CARE (Choquet et al. 2009a). The overall GOF was not statistically significant, thereby indicating a good fit to the data (chi^2=34.34, 43df, p=0.824). Our starting model considered the interaction among time, habitat and age on survival and the interaction between habitat and time on recapture. We started model selection by testing the effects of time, habitat and effort (differentiating years of low fieldwork effort "2007 and 2008" and years with intense fieldwork effort "2009 to 2017") on recapture while maintaining survival as in the starting model. Once the best structure for recapture was selected, we modelled the effects of habitat and time on survival. Then, using the previous selected structure of survival and recapture parameters, we tested the effect of family structure on future juvenile and adult survival of the offspring. Models were implemented in program E-SURGE 2.1.4 (Choquet et al. 2009b).

Model selection

Model selection was performed using Akaike Information Criterion corrected for small sample sizes, AICc (Burnham and Anderson 2002). Within each set of models (which includes the null model), we calculated the ΔAICc (as the difference between the AICc of model i and that of the best model) and the Akaike weight (w) of each model. Models within 2 AICc units of the best one were considered as alternatives and used to perform model averaging (MuMIn package, Barton 2017). We considered that a given effect received no, weak or strong support when the 95% confidence interval (CI) strongly overlapped zero, barely overlapped zero, or did not overlap zero, respectively.

Results

Delayed dispersal and kinship

During our study period we monitored 5518 breeding events, of which 251 events (4.5% of total) corresponded to breeding units formed by more than 2 individuals (hereafter, cooperative units). Cooperative breeding events occurred all the breeding seasons but were a less common breeding strategy. Most cooperative units (almost the 97%) included only one additional male, while in 3% of the cases we recorded 2 additional birds (2 males, 1 male and 1 female, or 2 females).

Ringing data show that these extra-individuals were close relatives (offspring) of the main breeders, both when the social identity of all individuals was known (the additional individuals and the main male and female, n = 12) as well as when only one of the breeder was of known identity (n = 22 cases). These individuals are grown offspring with delayed dispersal, postponing the settlement in their own breeding territories. Genetic parentage analysis performed in 5 families where all the 3 adults were ringed and bled corroborate that the additional members of the cooperative units were offspring of the main breeders.

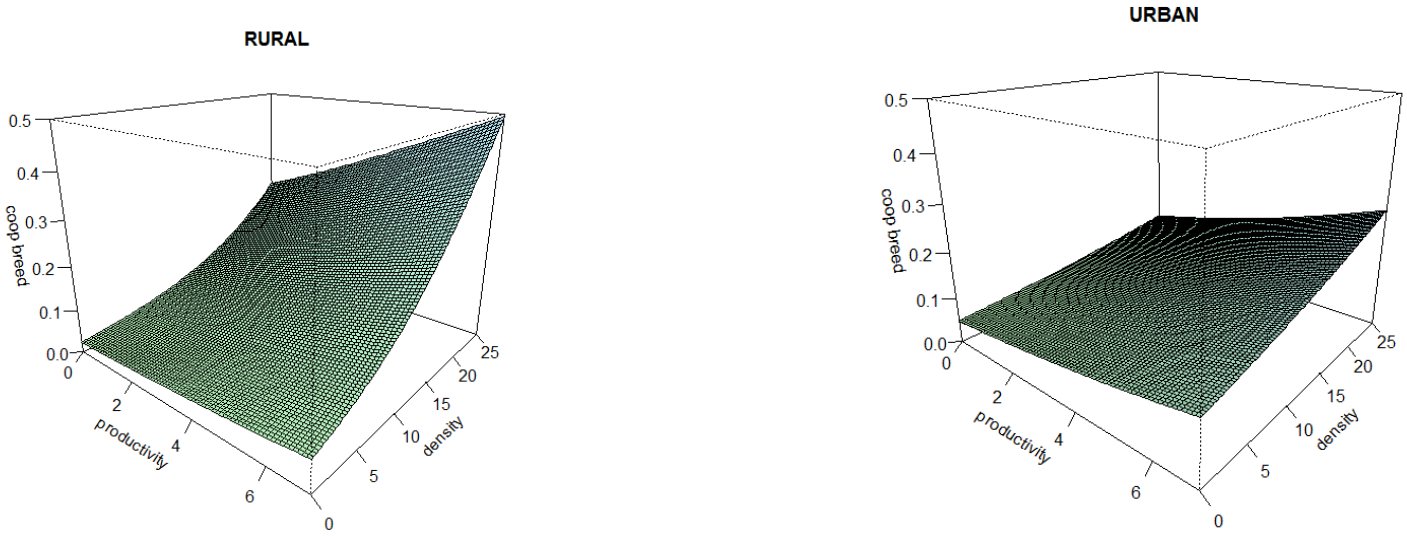
Ecological correlates that drive cooperative breeding

Territories located in urbanized areas were more prone to host cooperative reproductive structures (5.2% of the monitored breeding events) than territories in rural areas (2.1% of the monitored breeding events). Productivity, conspecific density, habitat type and the interaction between conspecific density and habitat had influenced the probability of occurrence of cooperative breeding (Model 1, w=0.40; Table 1). Cooperative breeding is developed in most cases in the city, but we detected a significant and negative effect of the interaction between the habitat and the conspecific density, so that the probability to form alternative breeding structures was especially high in densely occupied rural areas (Figure 1). Finally, although two other alternative models including additional interactions were close to the best supported model in terms of AICc, the effects of these additional interactions were not significant (Models 2 and 3; SP2).

Table 1. Modelling the effects of habitat (hab), productivity (product), and conspecific density (consp.density) on the probability to develop cooperative breeding in burrowing owls Athene cunicularia. Only models with an AICc weight >0 are shown (the complete series of model in SP1). df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc), w: Akaike weights.

Model	Family structure (n=5518)	Df	AICc	ΔAICc	w
Model 1	produc+hab+consp.density+ hab*consp.density	6	1941.62	0.00	0.40
Model 2	produc+hab+consp.density + hab*consp.density+hab*produc	7	1942.99	1.37	0.20
Model 3	produc+hab+consp.density + hab*consp.densityt+produc*consp.density	7	1943.47	1.85	0.16
Model 4	hab+consp.density+hab*consp.density	5	1944.62	3.00	0.09
Model 5	produc+hab+consp.density	5	1945.39	3.77	0.06
Model 6	produc+hab+consp.density+ hab*produc	6	1946.50	4.88	0.03
Model 7	produc+hab+consp.density+ produc*consp.density	6	1946.86	5.24	0.03
Model 8	produc+hab+consp.density+ hab*produc+produc*consp.density	7	1947.49	5.87	0.02

Figure 1. Cooperative breeding probabilities in urban and rural habitats according to the conspecific density and productivity in the area. Based in model averaged estimates. Coop breed= cooperative breeding; density= conspecific density; productivity= productivity in the area.



Brood condition, current fecundity and future brood survival

Following a model selection procedure the best supported model (Model 1, w= 0.86) revealed significant effects of habitat, breeding system and the interaction between the two variables in the body condition of chicks (Table 2). The coefficients relating brood condition with breeding system were positive (15.69, CI: 7.57, 23.82), indicating that chicks raised in cooperative breeding systems have better body condition. We found no significant effects of the habitat nor the interaction between the habitat and the breeding system in the brood condition.

Table 2. Relative importance of the breeding system (bi-parental vs. cooperative breeding) and habitat (rural vs. urban) on the body condition of chicks of burrowing owls *Athene cunicularia*. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models shown are those with w>0. Df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc), w: Akaike weights; coop. breed.= cooperative breeding.

Models	Body condition (n=1594)	Df	AICc	ΔAICc	w	Variables	Estimate	2.5%	97.5%
Model 1	habitat+ breeding system+ habitat*breeding system	6	14125.74	0.00	0.86	habitat (urban)	2.20	-0.57	4.96
Model 2	habitat + breeding system	5	14129.87	4.12	0.11	**breeding system (coop. breed.)**	**15.69**	**7.57**	**23.82**
Model 3	breeding system	4	14132.24	6.50	0.03	habitat*breeding system	-5.20	-14.88	4.49

The breeding success (probability of raise at least one chick) of burrowing owls differed between breeding system and habitats (Model 1, w= 0.65, Table 3A). Specifically, urban territories and territories including helpers had higher probability to breed successfully (Figure 2). Similarly, mating system and habitat also affected breeding productivity (Model 1, w= 0.59, Table 3B). The number of fledglings per nest was higher in territories occupied by cooperative breeders and in urban territories (Figure 2). Models including interactions between variables were close in terms of AICc but the effect of interactions was not statistically significant (Model 2A, Model 2B; Table 3. To see details SP3).

Table 3. Testing the effects of the breeding system developed (bi-parental vs cooperative breeding) and habitat on fecundity of burrowing owls. Df: degree of freedom; AICc: Akaike Information Criterion corrected for small sample sizes; ΔAICc: difference between the AICc of model *i* and that of the best model (*i.e*. the model with the lowest AICc), w: Akaike weights; null: null model.

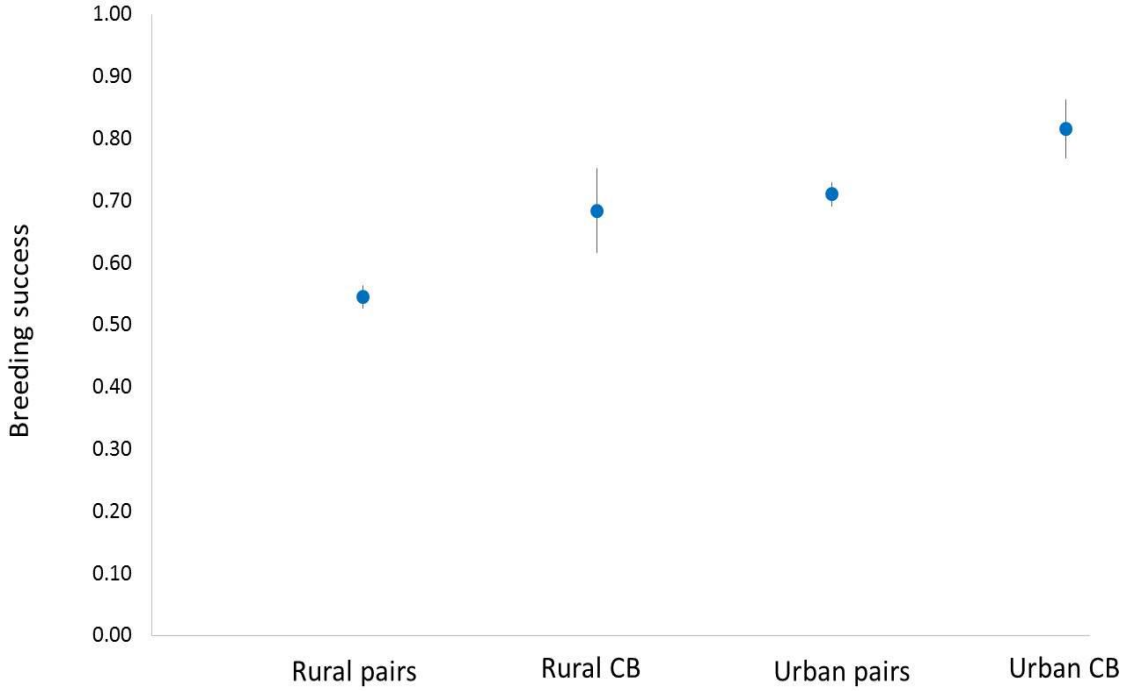
A) Breeding success

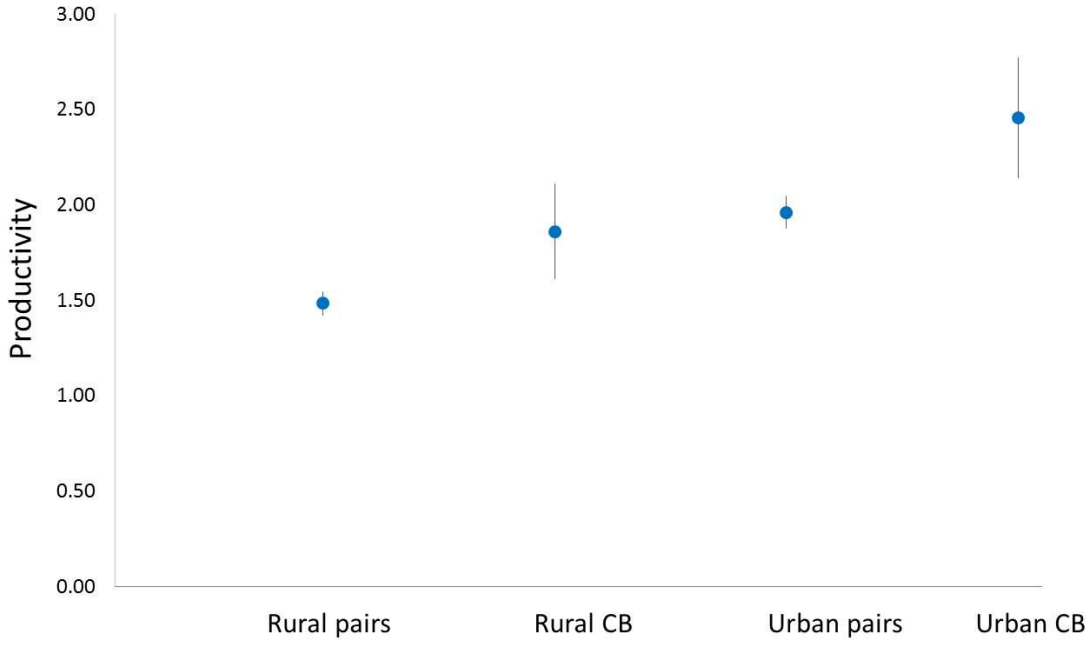
	Total (n=5043)	Df	AICc	ΔAICc	w
Model 1	habitat+breeding system	4	6405.50	0.00	0.65
Model 2	habitat+breeding system+ habitat*breeding system	5	6406.77	1.27	0.35
Model 3	habitat	3	6416.38	10.88	0.00
Model 4	breeding system	3	6549.90	144.41	0.00
Model 5	(null)	2	6569.24	163.75	0.00

B) Productivity

	Total (n=5043)	Df	AICc	ΔAICc	w
Model 1	habitat+breeding system	5	17804.87	0.00	0.59
Model 2	habitat+breeding system+ habitat*breeding system	6	17805.61	0.74	0.41
Model 3	habitat	4	17815.04	10.17	0.00
Model 4	breeding system	4	17892.19	87.32	0.00
Model 5	(null)	3	17908.63	103.77	0.00

Figure 2. Effects of breeding system (CB=cooperative breeding) and habitat on the breeding success (at least one chick per nest) and the productivity (number of fledglings per nest) of burrowing owls.



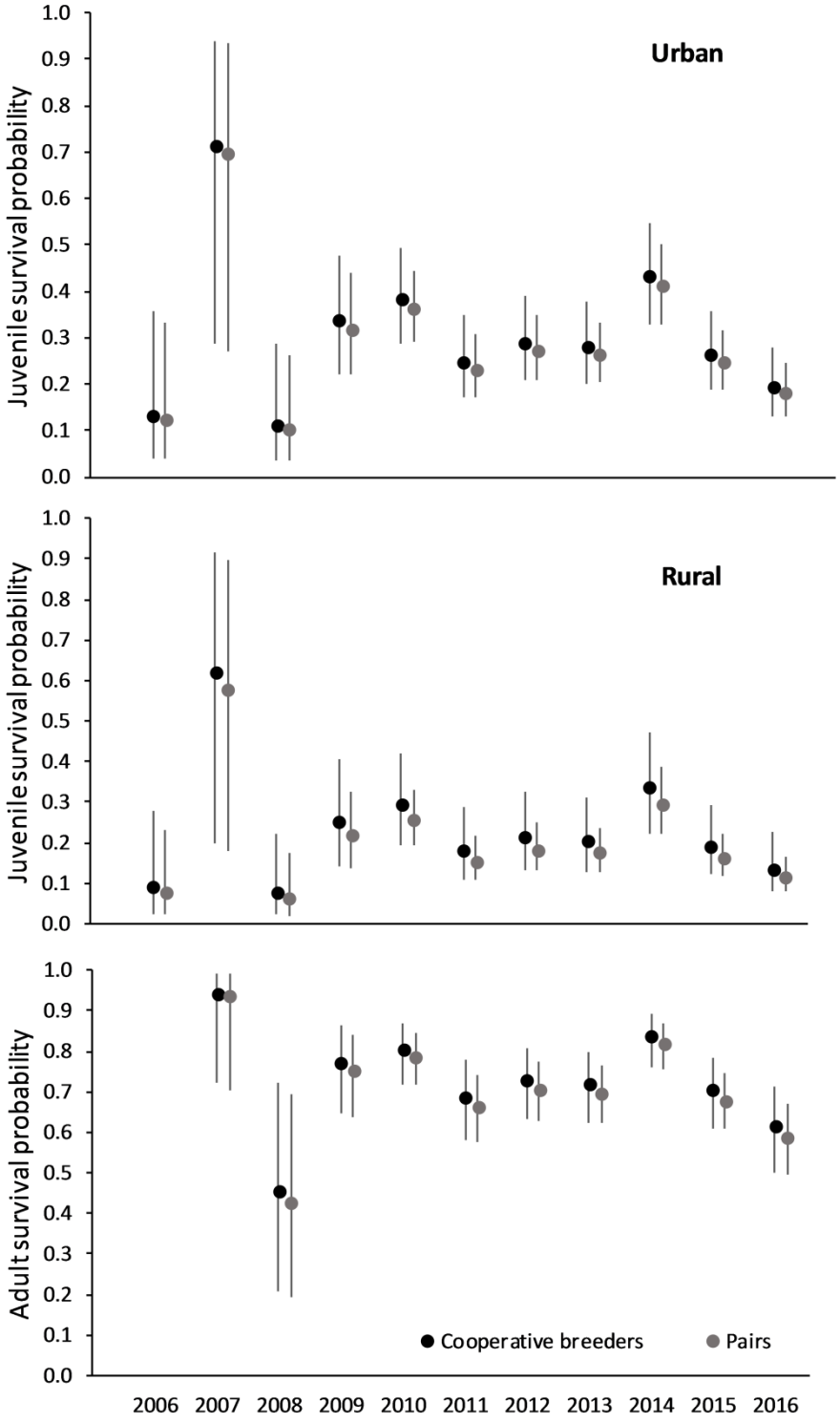


Capture-recapture analyses showed that recapture probabilities depended on the fieldwork effort but not on the habitat (SP4). Model averaged estimates of recapture probabilities were 0.4 for years 2007-2008 and 0.8 for years 2009-2017. The best model included an effect of year and habitat for juvenile survival probabilities and an effect of year for adult survival, both varying in parallel over time (Model8b, SP5). Adult survival was higher than juvenile survival, which was higher at urban areas than at rural ones (Figure 3). During the study period, mean survival for adults was 0.71 (95% CI: 0.60-0.79), mean survival for urban juveniles was 0.29 (95% CI: 0.19-0.41) and mean survival for rural juveniles was 0.21 (95% CI: 0.12-0.31) (Estimates from a model equivalent to model 1 but excluding the temporal variation in survival). Alternative models including the effect of breeding system (bi-parental vs. cooperative breeding) were close in terms of QAICc (Table 4). Model averaged estimates show that individuals raised in cooperative breeding structures showed a slight improve in their survival prospects compared with individuals raised by pairs, but the confidence intervals greatly overlapped (Figure 3).

Table 4. Modelling the effects of breeding system (bs), age (juv: juvenile; ad: adult) habitat (hab:habitat; urb:urban; rur:rural), and time (t) on survival. All models considered the effect of field effort on recaptures (SP4). AICc: Akaike Information Criterion corrected for small sample sizes; ΔAICc: difference between the AICc of model *i* and that of the best model (*i.e.* the model with the lowest AICc); Df= degrees of freedom; w= Akaike weights.

Model	Survival	Df	Deviance	QAICC	ΔAICC	w
Model 1	**(juv*hab/ad)+t**	**15**	**2782.13**	**2731.33**	**0**	0.27
Model 2	(juv*hab/ad)+bs+t	16	2780.46	2731.74	0.41	0.22
Model 3	(juv_{urb}/juvrur*bs/ad)+t	16	2781.14	2732.40	1.07	0.16
Model 4	(juv*hab/ad*bs)+t	16	2781.15	2732.41	1.08	0.16
Model 5	(juvurb*bs/juvrur/ad)+t	16	2781.89	2733.13	1.80	0.11
Model 6	(juv*hab*bs/ad)+t	17	2780.89	2734.20	2.86	0.06
Model 7	(juv*hab*bs/ad*bs)+t	18	2780.06	2735.42	4.09	0.03

Figure 3. Model averaged estimates (Table 4) of survival probabilities of adults, rural and urban juveniles raised in cooperative breeding systems (black) and bi-parental systems (grey). Bars indicate the 90% interval confidences.



Discussion

Delayed dispersal and kinship

In many vertebrate species, sexually mature individuals can postpone dispersal, and thus reproduction, to stay as subordinates in cooperative units, helping dominant individuals to raise their offspring (Cockburn 1998; Clutton-Brock 2002). Our genetic and fieldwork data suggest that the adults involved in cooperative breeding systems are more related among them than those breeding in typical pairs. The extra adults are grown offspring, mainly males, which delay their natal dispersal to remain in the same territory with one or both parents. This finding is in agreement with consistent evidences obtained in more species around the world, which show how cooperative breeding occur in the majority of the cases between family members (Komdeur 1994; Russell and Hatchwell 2001; Nam et al. 2010; Cockburn 2006; Hatchwell 2009; Browning et al. 2012). Rodriguez- Martínez et al. (2014) confirmed the high rate of monogamy for this species in the study area, but we have no evidence that this trend vary when more than two adults directly collaborate in a single nest.

Ecological correlates that drive cooperative breeding

The factors that influence the development of cooperative breeding have been intensively investigated in social species, where the frequency of delayed dispersal and, thus, cooperative units, is rather high (Hatchwell and Komdeur 2000; Hatchwell 2009; Jetz and Rubenstein 2011). However, delayed dispersal and cooperative breeding have been also described in some non-social species (i.e. Carrete et al. 2006), puzzling our knowledge on why should one individual help another at an expense to itself, and suggesting that there may not be a general explanation but rather a dynamic and taxonomically varied combination of factors influencing the evolution and maintenance of this strategy. Our results provide evidence that in a typical monogamous species, the habitat, together with conspecific density and the productivity in the breeding area, may influence reproductive decisions, driving the

development of cooperative breeding strategies. Previous research conducted on this species and study area indicates that the demographic trends and selective pressures vary between habitats and within them. Thus, higher breeding densities occur in high quality zones with low predation pressure, mainly in the city and certain rural patches (see details in Rebolo- Ifrán et al. 2017). In this sense, our results indicate that cooperative breeding is twice more common in the city; however, in high dense rural areas cooperative breeding also occur, and with high probabilities. The role of the ecological constraints as explanation for the development of cooperative breeding has been widely accepted in birds (Koenig et al. 1992; Emlen 1994). The high selective pressures observed in certain patches in our rural area may hinder or impede the successful settlement in marginal territories (Sergio and Newton 2003; Farrell et al. 2012). Certainly related to this, in areas with heterogeneous habitat quality the direct fitness benefits of independent breeding in poor quality patches may not outweigh the indirect inclusive fitness gains of remain in the natal territory (inheritance of natal or very close territories) (Stacey and Ligon 1991, Komdeur 1992; Pen and Weissing 2000). These ecological factors may explain why the delayed dispersal of some young males and the subsequent development of cooperative strategies emerge with major probability in high quality territories (Stacey and Ligon 1987; Komdeur 1992; Hatchwell and Komdeur 2000).

Brood condition, current fecundity and future brood survival

The additional adults involved in cooperative breeding can contribute in different reproductive related tasks, from egg incubation to territory defense (Boland 1998; Maklalov 2002). However, helper behavior may be specialized or mainly focused in one single labor, instead of divided in all the possible tasks (Arnold et al. 2005). Our results revealed that chicks raised with the help of extra adults have better body condition, suggesting that the role played by the helper could be related with food provisioning. Moreover, in a previous study conducted with this species in the same study area, Lois (2013) showed that helpers did not actively participate in or increase the effectiveness

of nest defense (indeed, individuals in cooperative units took longer to approach the predator and performed less aggressions toward it than breeding pairs), suggesting that the helping behavior conducted by the additional adult is focused to offspring food provisioning.

The contribution of helpers in cooperative breeding units can affect the reproductive success of the nests in which this reproductive system occur, but the overall contribution of helpers in this sense is variable: they can have positive but also irrelevant effects on the reproductive output (Hatchwell 1999*;* Legge 2000; Eguchi et al. 2002; Hatchwell et al. 2004; Blackmore and Heinsohn 2007). In this sense, Magrath and Yezerinac (1997) showed that the presence of additional adults involved in reproductive tasks in the white-browed scrubwrens (*Sericornis frontalis*) does not lead to an increase in the reproductive success of this species. On the contrary, Woxvold and Magrath (2005) and Kingma et al. (2010) have demonstrated the reproductive benefits of cooperative breeding in the apostlebird (*Struthidea cinerea)* and the purple-crowned fairy-wren (*Malurus coronatus)* respectively. In our case, the presence of helpers clearly enhanced the fledgling production of burrowing owls, probably via the potentially higher body condition or quality of individuals raised by cooperative breeding. This suggests that the contribution of an extra adult can be of greater value.

The assistance of non-breeder adults may also influence the survival of the offspring (Bennun, 1994; McGowan et al. 2003; Ridley 2007; Lloyd et al. 2009; Meade et al.2010). However, the effects of helper individuals in this component of fitness are much difficult to detect than immediate reproductive consequences (Emlen 1991; Arnold and Owens 1998). Here, using a long term monitoring on marked individuals, we show that survival rates slightly increase for individuals raised with the help of extra adults. The small advantage of birds raised by cooperative breeding systems may be due to the better body condition acquired as nestling when helpers collaborate in food provisioning. However, after independence, selection pressures not related with the body condition may affect similarly birds raised in bi-parental families or in

cooperative system, hence the scarce differences observed in terms of survival (Woxvold and Magrath 2005).

Conclusion

Here we show how social related factors and changes associated to human habitat transformation can promote delayed dispersal to develop cooperative breeding behavior in a typically bi-parental species. Genetic analyses and resights of marked individuals suggest a high kinship between the adults involved in cooperative breeding events. The existence of high quality areas, mainly located in the city and in certain patches of natural areas, may determine the formation of alternative breeding systems. The potential benefits of cooperative behavior emerge mostly the form of better reproductive results and body condition of chicks in such territories with helpers, but only a slight improvement of better survival probabilities of the offspring was detected. The fact that reproductive capable adults delay their dispersal reinforces the idea that this species show a low dispersal tendency. Further research is needed to evaluate the fitness benefits for the helper and for the breeders along their lifetime.

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Chapter 3

“Personality-dependent breeding dispersal in rural but not urban burrowing owls.”

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Personality-dependent breeding dispersal in rural but not urban burrowing owls

Abstract

Dispersal propensity has been correlated with personality traits, conspecific density and predation risk in a variety of species. Thus, changes in the relative frequency of behavioural phenotypes or in the ecological pressures faced by individuals in contrasting habitats can have unexpected effects on their dispersal strategies. Here, using the burrowing owl *Athene cunicularia* as a study model, we test whether changes in the behavioural profile of individuals and changes in conspecific density and predation pressure associated with urban life influence their breeding dispersal decisions compared to rural conspecifics. Our results show that breeding dispersal behaviour differs between rural and urban individuals. Site fidelity was lower among rural than among urban birds, and primarily related to an individual's behaviours (fear of humans), which has been reported to reflect individual personality. In contrast, the main determinant of site fidelity among urban owls was conspecific density. After taking the decision of dispersing, urban owls moved shorter distances than rural ones, with females dispersing farther than males. Our results support a personality-dependent dispersal pattern that might vary with predation risk. However, as multiple individuals of two populations (one urban, one rural) were used for this research, differences can thus also be caused by other factors differing between the two populations. Further research is needed to properly understand the ecological and evolutionary consequences of changes in dispersal behaviours, especially in terms of population structuring and gene flow between urban and rural populations.

Introduction

Dispersal has important consequences for an individual's fitness, affecting population structure, species distributions, and range shifts (Greenwood and Harvey 1982; Pasinelli et al. 2007). Thus, understanding why and how organisms disperse is central to many questions in theoretical and applied ecology and evolution (Serrano et al. 2001; Bowler and Benton 2005). Breeding dispersal (i.e. the inter-annual movement of individuals between breeding sites) has received much attention in recent decades, especially for birds. Within this taxonomic group, breeding dispersal has been related to an individual's characteristics such as age or sex, suggesting differences in gender roles in territory acquisition (Greenwood and Harvey 1982) as well as benefits derived from breeding-site familiarity (Newton and Marquiss 1982; Forero et al. 1999; Serrano et al. 2001). However, within a sex or age class, individual variation in dispersal movements can be important and linked to an individual's experience such as breeding success, mate loss, or predation pressure in the previous year (Pasinelli et al. 2007; Ganey et al. 2014; Payo-Payo et al. 2018), which can be ultimately influenced by habitat quality (Payo-Payo et al. 2017) and modulated by conspecific density (Hammill et al. 2017). A recent theory has suggested that individual variation in dispersal may also be linked to individual differences in behavioural types or behavioural syndromes that can be stable over the ontogeny or across situations (defined as a given set of conditions at one point in time, involving different levels along an environmental gradient or different sets of conditions across time; Sih et al.2004), leading a personality-dependent dispersal (Clobert et al. 2009; Denoël et al. 2017). However, as behavioural differences between individuals usually influence their vulnerability to predation (Jones and Godin 2009; Harris et al. 2010) the pattern of personality-dependent dispersal can be modified when factors motivating dispersal, such as predation risk, change (Cote et al. 2013). Thus, studies contrasting dispersal patterns of conspecifics subjected to different selection regimes can help us better understand the dynamic nature of dispersal as well as its drivers. This is particularly important in the

context of global change, as dispersal is a crucial mechanism allowing species to respond to shifting environmental conditions (Payo-Payo et al. 2018).

Urbanisation is one of the most prevailing causes of habitat transformation worldwide and a main driver of global change. Although animal communities are usually simplified and homogenised in these new habitats (Sol et al. 2014), cities can also act as predator-free refuges for the many species able to colonise them (Rebolo-Ifrán et al. 2017). This colonisation of urban environments by birds has been related to their inter-individual variability in fear of humans (a repeatable and heritable behaviour which is correlated with exploration and antipredatory behaviour and can be considered as a personality trait; Carrete and Tella 2013; Carrete et al. 2016), such that urban life would select for fearless individuals (Carrete and Tella 2010; Carrete and Tella 2017). In urban areas, these individuals can improve their demographic parameters, as predation risk is lower, and establish larger population densities than in rural habitats, even changing the habitat selection pattern of a species (Carrete and Tella 2011; Møller 2012). However, due to the role of behaviour, conspecific density and predation pressure on the dispersal propensity of individuals, urbanisation can deeply affect not only the demography but also the spatial structure and dynamics of rural and urban populations. In spite of this, studies comparing breeding dispersal behaviour of individuals living in both habitat types are scarce (Marzluff et al. 2016) and no one has deeply explored the mechanism provoking these differences.

Here, using the burrowing owl *Athene cunicularia* as a study model, we assessed the importance of an individual's traits (age, sex, and behaviour), previous breeding experiences (breeding output and nest predation) and conspecific density in determining individual breeding dispersal behaviour in rural and urban birds. We specifically considered how an individual's personality affects site fidelity and breeding dispersal distances, discussing which changes associated with urban life (i.e. reduction in predation pressure, increments in conspecific density or selection of individuals tolerant towards humans) can explain differences in the dispersal patterns of rural and urban birds. Our results showed that rural birds were less faithful to their breeding territories and dispersed at greater distances than urban ones. Our findings support

the personality-dependent dispersal hypothesis and a role for the behavioural skewness associated with urban invasion in explaining changes in dispersal patterns of urban and rural birds, highlighting the potential of urbanisation to cause population structuring by altering individual's movements.

Material and methods

Study species and area

The burrowing owl is distributed across American open landscapes, breeding in burrows excavated by the owls themselves or by mammals. Breeding pairs are territorial and show diurnal activity, and are easily located in the surroundings of their nests (Carrete et al. 2016). In our study area (ca. 5,400 km^2 of rural and urban areas around Bahia Blanca city, Argentina), rural owls breed in large extensions of natural grasslands and pastures dedicated to extensive livestock grazing and low-intensive cereal crops, where human presence is extremely low and mostly restricted to a few paved or unpaved roads (Rebolo-Ifrán et al. 2015). Urban owls, conversely, excavate their nests in small private and public gardens in urbanised residential areas, unbuilt spaces among houses, curbs of streets and large avenues, and are in constant contact with homeowners, children, pedestrians and intense car traffic. The city is immediately surrounded by large and flat rural extensions, with no obstacles preventing owls from moving between habitats (Carrete and Tella 2013). Moreover, as owls are able to excavate their own burrows, there are no habitat constraints (e.g., availability of nesting structures) that can limit their dispersal movements.

From 2006 to 2016, we annually monitored the breeding population of the species in the study area, totalling ca. 2,200 urban and 3,000 rural nests during the whole period. The location of all occupied nests was used to calculate an annual aggregation index for each breeding pair as their relative position within the spatial distribution of all breeding pairs[32]. This index, which reflects conspecific density, was obtained as $S_i = \Sigma \exp(-d_{ij})$ (with $i \neq j$), where d_{ij} was the linear distance between pairs i and j. Territories

were repeatedly visited to assess breeding success (i.e. breeding pairs successfully producing at least one fledgling) and productivity (i.e. the number of young fledged per breeding attempt), and to look for signs of predation such as the presence of corpses or plucked owl feathers at the entrance of the nests (see Rebolo-Ifrán et al. 2017 for a more detailed methodology). During this period, we also captured ca. 2,000 adults and chicks using bow nets and ribbon carpets to mark them with plastic colour-numbered rings readable at distance. Individuals were sexed based on plumage characteristics (Carrete and Tella 2011) and, when needed, by molecular procedures (Rodriguez-Martínez et al. 2014). Resightings of marked birds were done during an intensive population monitoring program lasting from 2007 to 2016, surveying all known breeding sites as well as unoccupied but suitable areas. Fear of humans is indicative of the risk that individuals are willing to take in our presence, and has been shown to be key to understanding avian urban invasion (Carrete and Tella 2011). This behaviour is highly repeatable along an individual adulthood (Carrete and Tella 2013), heritable (Carrete et al. 2016) and linked to exploration and antipredatory behaviours (Carrete and Tella 2017), and is thus a consistent predictor of individual personality. We measured fear of humans of breeding birds during the chick-rearing period as the distance at which individuals flee when approached by a human (so-called flight initiation distance, hereafter FID), following standard protocols (see details in [Rebolo-Ifrán et al. 2017; Carrete et al. 2016]). Both single and average values of FID were used (when more than one measure was obtained from a single individual in the same or different years), given the high repeatability of this behaviour (Carrete and Tella 2013).

Statistical approach

We used Generalized Linear Mixed Models (GLMM) to compare site fidelity (logistic link function, binomial error distribution) and dispersal distances (log-transformed, identity link function, normal error distribution) between rural and urban owls and to explore the effects of individual traits (sex, age, and FID), previous breeding experience (breeding success, productivity and predation), and conspecific density on these parameters. We considered that a bird remained faithful to its previous-year breeding site when it stayed in the same nest or in its immediate surroundings (radius=10m)

between successive breeding events. This distance was established based on the GPS location error (3-8 m) and given that holes at distances ≤10 m can be different entrances to the same burrow. For individuals moving farther than 10 m (categorized as dispersers), we measured their dispersal distances as the straight- line between two consecutive breeding sites.

We assessed the relative contribution of individual traits, previous experience and conspecific density in determining the dispersal patterns of rural and urban burrowing owls using an information-theoretic approach on two main datasets. First, we performed models using the group of individuals of known age (captured as chicks in their nests), to explore the role of age in dispersal. Then, as most individuals were captured as adults and their age was unknown, we ran a second set of models without considering the effect of age. Models were built using a different combination of variables in interaction with habitat, but including alternatively only one descriptor of an individual's previous experience due to their high correlational causation (predation is the main cause of breeding failure in the study species, thus affecting breeding success and productivity, see details in Rebolo- Ifrán et al. 2017) and multicollinearity. All models included "individual" and "year" as random terms to control for pseudoreplication and potential interannual differences, respectively.

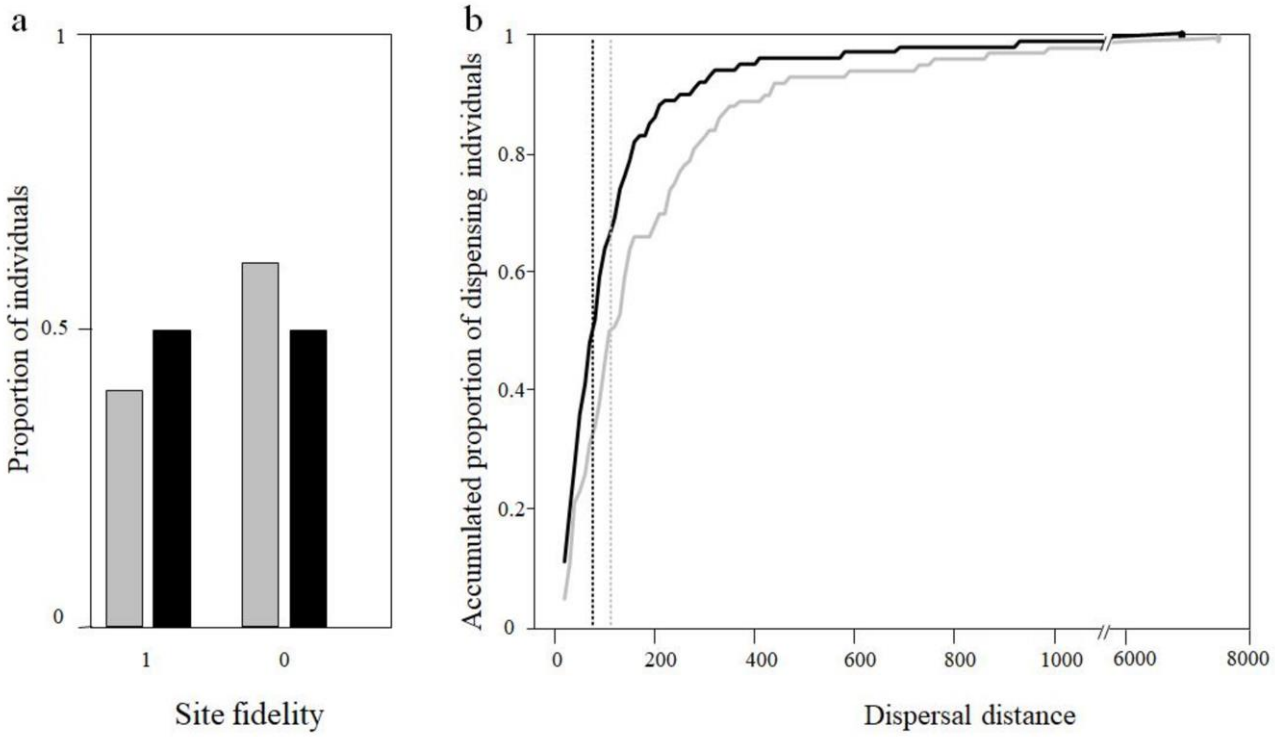
Model selection was performed using the Bayes Information Criterion, BIC (Burnham and Anderson 2002). Within each set of models (which includes the null model), we calculated the ΔBIC*i* (as the difference between the BIC of model *i* and that of the best model) and the weight (*w*) of each model. Models within 6 BIC units of the best one were considered as alternatives and used to perform model averaging (MuMIn package; Barton 2017). BIC penalizes larger models more heavily than other criteria such as the Akaike Information Criteria (AIC) and so will tend to prefer smaller models sometimes losing some weak relationships. Thus, we also used the AICc (Akaike Information Criterion corrected for small sample sizes) to checked the consistency of our findings (results obtained using AICc are only shown in Supplementary Materials). All continuous variables were centred before modelling to properly estimate their main effects regardless of whether we include the interaction (Grueber et al. 2011).

We considered that a given effect received no, weak or strong statistic support when the 95% confidence interval (CI) strongly overlapped zero, barely overlapped zero, or did not overlap zero, respectively. Complementarity, we calculated the coefficient of determination, R^2, as a measure of the variance explained by a model (Nakagawa and Schielzeth 2012). Statistical analyses were conducted in R 3.1.2 (R Development Core Team R 2008).

Results

We recorded 866 breeding dispersal events in 130 rural and 334 urban owls. Rural birds were less faithful to their breeding sites (rural: 39%, urban: 50%; χ^2= 6.23, d.f. = 1, p=0.0126; Figure 1a) and, when they dispersed, did so at greater distances than urban birds (median rural: 112m, range: 13-7,500m, median urban: 76.5m, range: 11-6,900m; $F_{1,348}$ = 40.67, p < 0.0001; Figure 1b).

Figure 1. (a) Proportion of burrowing owls showing site fidelity (1) or changing their breeding sites between successive years (0) in rural (grey bars) and urban (black bars) habitats. (b) For individuals changing their breeding sites, the accumulated proportion of dispersing urban (grey line) and rural (black line) individuals as a funciton of distance is also shown. The maximum dispersal distance observed is indicated by a point (grey and black, for urban and rural birds respectively). Vertical dashed lines show mean distances for urban (grey line) and rural (black line) birds.



Our reduced dataset of birds ringed as chicks show that age was not related to site fidelity or dispersal distance among urban and rural birds (Table 1 and S1).

Table 1. Alternative models (ΔBIC < 6) obtained to assess the relative importance of individual's traits (age, sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls *Athene cunicularia*. Models were run using information from individuals of known age (ringed as chicks). See Table S1 for alternative models obtained using the Akaike Information Criterion corrected for small sample sizes (AICc).

site fidelity	Df	BIC	ΔBIC	weight
null	3	211.19	0.00	0.36
productivity(t-1)	4	213.96	2.78	0.09
predation(t-1)	4	214.13	2.94	0.08
breeding success(t-1)	4	214.31	3.13	0.08
habitat	4	215.31	4.13	0.05
sex	4	215.55	4.36	0.04
aggregation	4	216.07	4.89	0.03
FID	4	216.16	4.97	0.03
habitat*FID	5	216.40	5.22	0.03
dispersal distance	**Df**	**BIC**	**ΔBIC**	**weight**
null	4	75.44	0.00	0.68
habitat	5	78.25	2.81	0.17

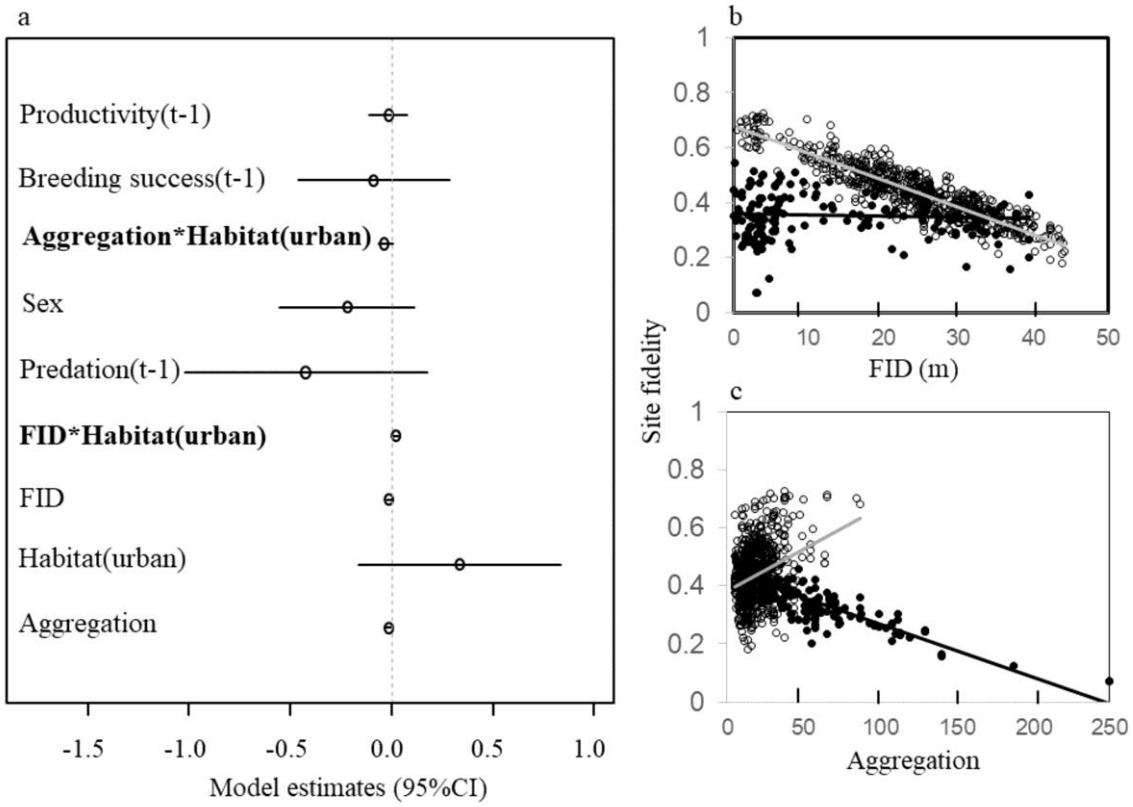
Thus, we relied on our larger sample including all individuals to assess the relative importance of an individual's traits, previous experience and conspecific density on the dispersal pattern of individuals. Using this dataset, we obtained alternative models including individual traits as well as descriptors of previous experience (Table 2). After model averaging, we found strong support for an effect of individual behaviour on site fidelity of rural birds and of conspecific density on site fidelity of urban and rural ones (Table 2; Figure 2), shyer rural individuals and birds breeding at higher conspecific densities having a higher probability of changing their breeding sites between successive years than their counterparts (R^2 = 0.16). Habitat, and breeding success and productivity in the previous year received strong support to explain variability in the dispersal distance of all individuals (R^2 = 0.46), urban birds, and individuals breeding successfully or having more chicks moving less than rural, and unsuccessful owls (Table 2; Figure 2). Models obtained using AICc show similar results, also supporting a role for conspecific aggregation in site fidelity of urban birds and sex on dispersal distance (females dispersing further than males; Table S2).

Table 2. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls *Athene cunicularia*. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models were run using all individuals of unknown age, as age has not received statistical support (see Table 1 and S1). Models shown are those used for model averaging (ΔBIC ≤ 6). See Table S2 for results obtained using the Akaike Information Criterion (ΔAICc < 6).

Site fidelity	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
FID	4	1083.00	0.00	0.30	**FID**	**-0.01**	**-0.02**	**0**
habitat	4	1084.18	1.18	0.17	**habitat(urban)**	**0.51**	**0.08**	**0.94**
null	3	1084.69	1.69	0.13	**FID*Habitat(rural)**	**-0.02**	**-0.03**	**-0.01**
habitat*FID	5	1085.70	2.70	0.08	FID*Habitat(urban)	0	-0.01	0.02
FID+predation(t-1)	5	1087.57	4.57	0.03	predation(t-1)	-0.44	-1.04	0.16
aggregation+ FID	5	1087.81	4.81	0.03	**aggregation**	**-0.01**	**-0.03**	**0**
habitat, FID	5	1088.03	5.03	0.02	sex(female)	-0.24	-0.57	0.09
sex, FID	5	1088.15	5.15	0.02				
sex	4	1088.46	5.47	0.02				
habitat+sex	5	1088.76	5.76	0.02				
habitat+ aggregation	5	1088.84	5.84	0.02				

Dispersal distance	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
habitat +breeding success(t-1)	6	471.18	0.00	0.53	**habitat(urban)**	**-0.22**	**-0.37**	**-0.07**
habitat	5	472.78	1.61	0.24	**breeding success(t-1)**	**-0.19**	**-0.35**	**-0.04**
breeding success(t-1)	5	476.05	4.88	0.05	breeding success(t-1)*habitat(urban)	0.21	-0.01	0.43
habitat*breeding success(t-1)	7	476.07	4.90	0.05	**productivity(t-1)**	**-0.04**	**-0.06**	**-0.01**
habitat*breeding success(t-1)	7	476.07	4.90	0.05				
habitat+productivity(t-1)	6	477.05	5.88	0.03				

Figure 2. (a) Factors affecting site fidelity among rural and urban burrowing owls (estimate ± 95% CI). Site fidelity was negatively related to individual behaviour (measured as flight initiation distances, FID) among rural individuals (b), while it was negatively related to conspecific density (measured as aggregation) among urban ones (c). Lines (black: rural, grey: urban) show the probability of remaining in the same breeding site for individuals with different FID and living at different conspecific densities. Dots (black: rural, white: urban) show predicted values.



The lack of support for individual behaviour explaining site fidelity among urban birds could be a consequence of the reduced variability shown by this variable compared to values observed among rural individuals (range FID: rural: 5 – 250 m, urban: 5 – 87 m). However, when models were run using a subset of rural individuals with FIDs within the range of urban birds, the results remained similar, and rural, shy individuals were still less faithful to their breeding sites than bolder (Table 3; R^2 = 0.10). Accordingly, individuals breeding successfully also dispersed at lower distances than unsuccessful ones (Table 3 and S3; R^2 = 0.57).

Table 3. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural burrowing owls *Athene cunicularia* with FID within the range of urban ones (5- 87m). Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models shown are those used for model averaging (ΔBIC ≤ 6). See Table S3 for results obtained using the Akaike Information Criterion (ΔAICc < 6).

Site fidelity	**df**	**BIC**	**ΔBIC**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
FID	4	210.05	0.00	0.29	**FID**	**-0.39**	**-0.76**	**-0.02**
null	3	210.09	0.03	0.29	sex (female)	-0.39	-1.11	0.32
sex	4	213.36	3.30	0.06	productivity(t-1)	-0.15	-0.5	0.19
FID, productivity(t-1)	5	214.23	4.18	0.04	breeding success(t-1)	-0.34	-1.1	0.42
breeding success(t-1)	4	214.24	4.19	0.04	aggregation	0.12	-0.22	0.46
FID, breeding success(t-1)	5	214.27	4.22	0.04	predation(t-1)	-0.42	-1.57	0.72
productivity(t-1)	4	214.29	4.24	0.03				
sex, FID	5	214.41	4.35	0.03				
aggregation	4	214.43	4.37	0.03				
predation(t-1)	4	214.48	4.43	0.03				
FID, predation(t-1)	5	214.50	4.45	0.03				
aggregation, FID	5	214.73	4.67	0.03				
Dispersal distance	**df**	**BIC**	**ΔBIC**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
breeding success(t-1)	5	114.18	0.00	0.92	breeding success(t-1)	-0.40	-0.60	-0.20

Discussion

Our results show that determinants of breeding dispersal differ between rural and urban burrowing owls. Site fidelity among rural birds was lower than among urban ones, and was primarily related to individual behaviour (measured here as fear of humans), such that shy individuals were more prone to changing their breeding sites between successive years than bold ones. This result challenges previous studies showing that emigrants, immigrants or colonizers are usually bolder, more exploratory, or aggressive than residents or locally born individuals (Fraser et al. 2001; Dingemanse et al. 2003). A potential explanation for this difference could be that, in our population, shy rural birds are also less aggressive toward predators (Carrete and Tella 2017), and may disperse from their breeding sites to avoid the abundant predators present in rural areas (Payo-Payo et al. 2018). Previous studies have shown that high predation pressure explained the reduced breeding success and productivity of this rural population compared to the urban one (Rebolo-Ifrán et al. 2017). Accordingly, we found a relationship between the experience of individuals in one year (breeding success and productivity) and their dispersal distance in the following year, so that unsuccessful individuals dispersed farther than successful ones. Contrary to rural birds, urban individuals were more faithful to their breeding sites and dispersed, in general, shorter distances during consecutive breeding seasons.

Moreover, the main determinant of site fidelity among urban individuals was conspecific density, such that individuals breeding at higher aggregations have a higher probability of dispersing than those occupying sparser areas. Positive density-dependent dispersal has been previously described in other taxa (Lèna et al. 1998; De Meester and Bonte 2010), and can arise due to competitive processes between the densely distributed urban pairs (ca. seven times higher than rural ones; Rebolo- Ifrán et al. 2017). However, no relationship between site fidelity or dispersal distance and individual behaviour was detected among urban owls. Although this result may be

related to the low variability in FID within urban birds, when rural individuals with profiles similar to those of urban birds were considered (i.e. FID ranging within values observed among urban birds: 0- 87 m), we still found a negative association between behaviour and site fidelity. This suggests more than a statistical issue, and that a personality-dependent dispersal pattern that varies between rural and urban habitats and is likely associated with predation risk is at play. Thus, in environments with high-predation risk (rural habitats), shy individuals, unlike bold ones, would be strongly limited in the number of suitable habitats (in terms of predation risk) they may occupy, thereby making behavioural differences between the two types more pronounced. On the contrary, predator release in urban environments would exert no constraints on individual movements, whatever their tendency to take risks, hence cancelling the personality-dependent dispersal pattern observed among rural individuals. Alternatively, or complementarily, it is also possible that the selection of bolder individuals during urban invasion could be dismantling the effect of personality on dispersal among urban individuals, as the absence of correlation between antipredatory behaviour and fear of humans among urban birds (Carrete and Tella 2017) could be reducing the relationship between fear of humans and dispersal in these habitats. It is worth mentioning that these results could have arisen as a consequence of differences in the resighting probability of birds related to personality and habitat type so that the covariance found in rural areas might represent an artefact caused by personality-related detection bias. However, our recapture probability in the study area is very high and not related to FID (see Supplementary materials).

Recent papers have explored how personality-dependent dispersal is affected in varying environments (Denoël et al. 2017), and its importance in spatial ecology and some global change scenarios, in particular, biological invasions and habitat fragmentation (Fogarty et al. 2011; Sih et al. 2012). Although urbanisation represents one of the most prevailing causes of habitat transformation worldwide and despite its profound effects on demography and behaviour (Marzluff et al. 2016; Tucker et al. 2018), there are no studies dealing with its potential role in changing the dispersal

patterns of individuals. At an interspecific level, previous studies have suggested a relationship between FID and descriptors of natal dispersal or range distribution (Lin et al. 2012; Møller and Garamszegi 2012). Here, we provide the first evidence, at the individual level, that breeding dispersal is also personality-dependent in a bird species, suggesting that changes in ecological conditions associated with urban life (increments in breeding success mainly through predation release, but also the selection of human-tolerant phenotypes) can dismantle this relationship, favouring site fidelity and short dispersal movements. This change in breeding dispersal behaviour is likely contributing to the genetic structure detected between three different urban and one panmictic rural populations of burrowing owls, but also between urban cores separated by a few kilometres (Mueller et al. 2018).

Our study has been performed using information on breeding dispersal at the individual level, controlling for the lack of independence in these data by including individual as a random term. These individuals, which belong to two separate groups (urban and rural), were compared and differences discussed in the context of changes associated to urban life. It is true that our study has been performed in only one urban-rural pair of populations, which prevent us to emphatically assess that differences in the dispersal patterns of our study units are due to urbanization. However, the contrasted characteristics of both habitats are tightly linked to their degree of urbanization, and differences observed among individuals living in urban and rural areas across the world have shown similar patterns than those obtained here and which have been related to dispersal in the present study (i.e., the bolder behaviour of urban individuals (Evans et al. 2011; Atwell et al. 2012; Miranda et al. 2013; Hardman and Dalesman 2018), the higher conspecific density of urban cores (Marzluff et al. 2001; Chace and Walsh 2006; Rodewald and Shustack 2008; Rodewald et al. 2011), the higher breeding parameters of urban compared to rural populations (Stracey and Robinson 2012) or the colonization of urban areas from a pool of rural individuals (Evans et al. 2009; Miranda et al. 2013). Thus, it is very likely that the dispersal patterns described here can be extended to other urban-rural areas. Further research,

however, is needed to make stronger generalizations to properly understand the ecological and evolutionary consequences of these differences in dispersal between urban and rural birds and its implications for population structuring and gene flow between urban and rural populations.

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III| Appendix

Chapter 1

Supporting information

Table S1. Relative importance of individual's traits (sex and personality, measured as FID), and social variables (conspecific density and productivity in the natal area) on the natal dispersal distances of rural and urban (habitat) burrowing owls *Athene cunicularia*. These models were run using individuals resighted during their first breeding attempts (n=189 individuals). Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero (asterisk), or did not overlap zero (in bold), respectively. Models shown are the first 10 models ranked using their AICc. Variable (*): model averaging performed using the subset of models that did not include habitat.

Model	**K**	**AICc**	**delta**	**weight**
FID + habitat + sex	6	500.79	0.00	0.28
conspecific productivity + FID + sex + habitat	7	502.45	1.66	0.12
conspecific density + FID + sex	6	505.89	1.87	0.14
conspecific density + FID + habitat + sex	7	502.78	1.98	0.10
habitat + sex	5	503.31	2.51	0.08
conspecific productivity*habitat + FID*habitat + sex*habitat	10	503.65	2.85	0.07
sex (*)	4	504.02	3.23	0.06
habitat*sex	6	504.06	3.27	0.05
FID*habitat + sex*habitat	8	504.33	3.54	0.05
conspecific density + sex (*)	5	504.99	4.20	0.03
conspecific productivity + habitat + sex	6	505.37	4.58	0.03
conspecific density + habitat + sex	6	505.39	4.59	0.03
FID + sex (*)	5	505.74	4.95	0.02

Variable	**Estimate**	**2.50%**	**97.50%**
FID	-0.18	-0.34	-0.02
habitat (urban)	-0.54	-0.94	-0.14
sex (females)	0.68	0.42	0.94
conspecific productivity	0.06	-0.08	0.19
conspecific density	-0.03	-0.19	0.12

Variable (*)	**Estimate**	**2.50%**	**97.50%**
sex (females)	0.61	0.35	0.88
conspecific density	-0.09	-0.24	0.06
FID	-0.06	-0.2'	0.08

Table S2. Relationship between natal dispersal distances and productivity during the first breeding attempt, and lifetime productivity of rural and urban (habitat) burrowing owls *Athene cunicularia*. These models were run using individuals resighted during their first breeding attempts (n=189 individuals). Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero (asterisk), or did not overlap zero (in bold), respectively. All models were run including year as a random term; models for lifetime productivity also included individual as a random term. Models shown are the first 10 models ranked using their AICc.

Productivity during the first breeding attempt

Model	K	AICc	ΔAICc	weight	Variables	Estimate	2.50%	97.50%
dispersal distance*sex + habitat	6	661.19	0.00	0.43	**dispersal distance**	**-0.67**	**-1.32**	**-0.01**
dispersal distance*sex	5	662.73	1.53	0.20	**sex (females)**	**0.49**	**0.17**	**0.80**
sex + habitat	4	663.84	2.64	0.11	habitat (urban)	0.29	-0.02	0.61
sex + dispersal distance*habitat	6	663.87	2.68	0.11	dispersal distance*sex (females)	0.68	0.02	1.35
sex + dispersal distance + habitat	5	665.66	4.46	0.05				
Sex	3	665.71	4.52	0.05				
sex + dispersal distance	4	667.42	6.22	0.02				
Habitat	3	668.04	6.85	0.01				
dispersal distance*habitat	5	668.12	6.93	0.01				
dispersal distance + habitat	4	670.12	8.93	0.01				

Lifetime productivity

Model	k	AICc	ΔAICc	weight	Variables	Estimate	2.50%	97.50%
sex + age	5	1239.58	0.00	0.20	**sex (female)**	**0.27**	**0.10**	**0.45**
sex + age	5	1239.58	0.00	0.20	**age**	**0.08**	**0.03**	**0.14**
sex + age + habitat	6	1240.69	1.11	0.11	habitat (urban)	0.11	-0.11	0.34
sex + age + habitat	6	1240.69	1.11	0.11	dispersal distance	0.02	-0.06	0.11
sex + age + dispersal distance	6	1241.34	1.76	0.08				

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sex + age + dispersal distance	6	1241.34	1.76	0.08				
				0.05				
sex + age + dispersal distance + habitat	7	1242.15	2.57					

Lifetime productivity

Model	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.50%**	**97.50%**
sex + age + dispersal distance*habitat	8	1242.48	2.90	0.05				
sex + age + dispersal distance*habitat	8	1242.48	2.90	0.05				

Chapter 2

Supporting information

Table S1. Modelling the effects of habitat (hab), productivity (product), and conspecific density (consp.density) on the probability to develop cooperative breeding in burrowing owls Athene cunicularia. df: degree of freedom, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc), w: Akaike weights.

Model	Df	AICc	ΔAICc	w
Produc +hab+ consp.density+ hab*consp.density	6	1941.62	0.00	0.40
produc+hab+consp.density + hab*consp.density+ hab*produc	7	1942.99	1.37	0.20
produc+ hab+ consp.density + hab*consp.densityt+ produc*consp.density	7	1943.47	1.85	0.16
hab+ consp.density+ hab*consp.density	5	1944.62	3.00	0.09
produc+ hab+ consp.density	5	1945.39	3.77	0.06
produc+ hab+ consp.density+ hab*produc	6	1946.50	4.88	0.03
produc+ hab+ consp.density+ produc*consp.density	6	1946.86	5.24	0.03
produc+ hab+ consp.density+ hab*produc+ produc*consp.density	7	1947.49	5.87	0.02
hab+ consp.density	4	1950.58	8.96	0.00
produc+ hab	4	1958.25	16.63	0.00
produc+ hab+ hab*produc	5	1959.06	17.44	0.00
produc+ consp.density	4	1964.17	22.54	0.00
Hab	3	1965.62	24.00	0.00
produc+ consp.density+ produc*consp.density	5	1966.13	24.51	0.00
consp.density	3	1971.60	29.98	0.00
produc	3	1995.02	53.40	0.00
(Null)	2	2008.97	67.35	0.00
predation	3	2010.10	68.48	0.00

Table S2. Relative importance of conspecific density (consp. density), productivity in the natal area, habitat type, and their interactions on the probability to develop cooperative breeding. Models shown are only those included within the best models by AIC in the Table 1 (Model 2 and 3).

Model 2	Estimate	Std.Error	Pr(>|z|)
intercept	-3.72	0.19	< 2e-16
consp.density	0.10	0.02	1.30e-05
productivity	0.20	0.09	0.03
habitat	0.76	0.15	4.84e-07
habitat*consp.density	-0.07	0.03	0.02
habitat *productivity	-0.10	0.13	0.42

Model 3	Estimate	Std.Error	Pr(>|z|)
Intercept	-3.72	0.19	< 2e-16
consp.density	0.10	0.02	4.18E-05
productivity	0.16	0.07	0.02
habitat	0.74	0.15	6.59E-07
consp.density*producivity	0.01	0.02	0.69
habitat*consp.density	-0.07	0.03	0.02

Table S3. Relative importance of the habitat type (urban vs. rural) and the breeding system (bi-parental vs cooperative breeding) on the breeding success and productivity of the burrowing owls *Athene cunicularia.* Only the model 2 in the two analyses was considered to be included within the best models by AIC.

Model2A	**Estimate**	**Std.Error**	**Pr(>|z|)**
Intercept	0.27	0.12	0.02
breeding system	0.40	0.25	0.10
habitat	0.72	0.06	<2e-16
habitat*breeding system	0.28	0.33	0.39

Model2B	**Estimate**	**Std.Error**	**Pr(>|z|)**
Intercept	0.40	0.04	< 2e-16
breeding system	0.34	0.12	0.004
habitat	0.29	0.03	< 2e-16
habitat*breeding system	-0.16	0.14	0.26

Table S4. Modelling the effects of age (a), habitat (hab), and time (t) on recapture probabilities. K: number of parameters estimated by the model; Eff: effort.

MODEL	SURVIVAL	RECAPTURE	K	DEVIANCE	QAIC	QAICC	ΔAICC
Model 1a	*a*hab*t*	*hab+t*	*52*	2732.65	2757.06	2759.80	7.82
Model 2a	*a*hab*t*	*hab+eff*	*45*	2741.82	2751.96	*2754.01*	2.03
Model 3a	*a*hab*t*	hab	44	2745.32	2753.37	2755.33	3.34
Model 4a	*a*hab*t*	t	51	2732.77	2755.18	2757.82	5.83
Model 5a	***a*hab*t***	**eff**	**44**	**2741.88**	**2750.02**	**2751.99**	**0**
Model 6a	*a*hab*t*	cte	43	2745.34	2751.38	2753.29	1.27

Table S5. Modelling the effects of age (a), habitat (hab), and time (t) on survival. juv: juvenile; ad:adult; eff:effort

MODEL	SURVIVAL	RECAPTURE	K	DEVIANCE	QAIC	QAICC	ΔAICC
Model 1b	a+hab+t	eff	15	2784.99	2733.87	2734.11	2.77
Model 2b	(a.hab)+t	eff	16	2782.03	2733	2733.26	1.93
Model 3b	a+t	eff	14	2794.60	2741.21	2741.41	10.08
Model 4b	a.t	eff	23	2779.36	2744.41	2744.95	13.62
Model 5b	a.hab	eff	6	2827.68	2757.32	2757.36	26.03
Model 6b	a+hab	eff	5	2831.25	2758.78	2758.81	27.48
Model 7b	a	eff	4	2843.86	2769.03	2769.05	37.71
Model 8b	**(juv.hab/ad)+t**	**eff**	**15**	**2782.13**	**2731.10**	**2731.33**	**0**
Model 9b	(ad.hab/juv)+t	eff	15	2794.08	2742.7	2742.94	11.60

Chapter 3

Supporting information

Table S1. Alternative models (ΔAICc < 6) obtained to assess the relative importance of individual's traits (age, sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls *Athene cunicularia*. Models are ranked using the Akaike Information Criterion corrected for small sample sizes (AICc).

Site fidelity	**df**	**AICc**	**ΔAICc**	**weight**
habitat*aggregation, habitat*sex, habitat*FID, productivity(t-1)	10	194.73	0.00	0.18
habitat*sex, habitat*FID, habitat*productivity(t-1)	10	195.61	0.88	0.12
habitat*aggregation, habitat*sex, habitat*FID, breeding success(t-1)	10	196.08	1.36	0.09
aggregation, habitat*sex, habitat*FID, productivity(t-1)	10	196.25	1.52	0.09
habitat*aggregation, habitat*sex, habitat*FID	9	197.35	2.62	0.05
habitat*sex, habitat*FID, habitat*breeding success(t-1)	10	197.49	2.77	0.05
aggregation, habitat*sex, habitat*FID, breeding success(t-1)	10	197.80	3.08	0.04
habitat*aggregation, habitat*sex, habitat*FID, predation(t-1)	10	198.06	3.33	0.03
habitat*sex, habitat*FID, habitat*predation(t-1)	10	199.29	4.56	0.02
aggregation, habitat*sex, habitat*FID	9	199.53	4.80	0.02
aggregation, habitat*sex, habitat*FID, predation(t-1)	10	200.05	5.33	0.01
Dispersal distance	**df**	**AICc**	**ΔAICc**	**weight**
null	4	66.62	0.00	0.26
habitat	5	67.22	0.60	0.19
habitat*breeding success(t-1)	7	67.78	1.16	0.15

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habitat*breeding success(t-1)	7	67.78	1.16	0.15

Dispersal distance	**Df**	**AICc**	**ΔAICc**	**weight**
predation(t-1)	5	70.58	3.96	0.04
sex	5	70.61	3.99	0.04
habitat, sex	6	70.97	4.35	0.03
habitat, predation(t-1)	6	71.27	4.65	0.03
breeding success(t-1)	5	71.43	4.81	0.02
habitat, breeding success(t-1)	6	72.10	5.48	0.02
sex, habitat*breeding success(t-1)	8	72.12	5.50	0.02

Table S2. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural and urban (habitat) burrowing owls *Athene cunicularia*. Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models were run using all individuals of unknown age, as age has not received statistical support (see Table 1 and S1). Models shown are those used for model averaging (ΔBIC ≤ 6).

Site fidelity	k	AICc	ΔAICc	weight	Variables	Estimate	2.5%	97.5%
aggregation, habitat*FID, predation(t-1)	7	1062.36	0.00	0.03	**aggregation**	**-0.01**	**-0.03**	**0**
habitat*FID	5	1062.44	0.08	0.03	predation(t-1)	-0.43	-1.15	0.29
habitat*FID, predation(t-1)	6	1062.44	0.08	0.03	**FID*habitat(rural)**	**-0.02**	**-0.03**	**0**
aggregation, habitat*FID	6	1062.53	0.17	0.03	FID*habitat(urban)	0.00	-0.01	0.02
sex, habitat*FID, predation(t-1)	7	1062.59	0.23	0.03	sex(female)	-0.27	-0.76	0.22
aggregation, sex, habitat*FID, predation(t-1)	8	1062.59	0.23	0.03	**FID**	**-0.01**	**-0.02**	**0**
sex, habitat*FID	6	1062.64	0.28	0.03	aggregation*habitat(rural)	0.01	-0.02	0.04

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aggregation, sex, habitat*FID	7	1062.81	0.45	0.03	**aggregation*habitat(urban)**	**-0.02**	**-0.04**	**0**

Site fidelity	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
habitat*aggregation, FID	6	1063.10	0.74	0.02	habitat(urban)	0.36	-0.25	0.96
habitat*aggregation, FID, predation(t-1)	7	1063.19	0.83	0.02	habitat(urban)*predation(t-1)	0.01	-1.38	1.4
habitat*aggregation, sex, FID	7	1063.52	1.16	0.02	habitat(urban)*sex(female)	0.28	-0.54	1.09
habitat*aggregation, sex, FID, predation(t-1)	8	1063.57	1.21	0.02	breeding success(t-1)	-0.09	-0.53	0.36
habitat, aggregation, FID	6	1063.79	1.43	0.02	productivity(t-1)	-0.01	-0.11	0.08
habitat, aggregation,FID, predation(t-1)	7	1063.81	1.45	0.02	habitat(rural)*productivity(t-1)	-0.07	-0.27	0.12
aggregation, habitat*FID, habitat*predation(t-1)	9	1064.27	1.91	0.01	habitat(urban)*productivity(t-1)	0.01	-0.10	0.11
aggregation, habitat*sex, habitat*FID predation(t-1)	10	1064.29	1.93	0.01	breeding success(t-1)*habitat(urban)	0.15	-0.73	1.03
aggregation, FID, predation(t-1)	6	1064.30	1.94	0.01				
habitat*FID, breeding success(t-1)	6	1064.31	1.95	0.01				
FID, predation(t-1)	5	1064.31	1.95	0.01				
aggregation, habitat*sex, habitat*FID	9	1064.32	1.96	0.01				
habitat, aggregation, sex, FID, predation(t-1)	8	1064.38	2.02	0.01				

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habitat*FID, productivity(t-1)	6	1064.39	2.03	0.01				
FID	4	1064.39	2.03	0.01				
Site fidelity	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
aggregation, habitat*FID, breeding success(t-1)	7	1064.40	2.04	0.01				
habitat, aggregation, sex, FID	7	1064.41	2.05	0.01				
aggregation, habitat*FID, productivity(t-1)	7	1064.48	2.12	0.01				
sex, habitat*FID, breeding success(t-1)	7	1064.51	2.15	0.01				
aggregation, FID	5	1064.55	2.19	0.01				
sex, habitat*FID, productivity(t-1)	7	1064.60	2.24	0.01				
habitat*aggregation, habitat*sex, habitat*FID	10	1064.63	2.27	0.01				
aggregation, sex, habitat*FID, breeding success(t-1)	8	1064.69	2.33	0.01				
sex, FID, predation(t-1)	6	1064.76	2.40	0.01				
aggregation, sex, habitat*FID, productivity(t-1)	8	1064.77	2.41	0.01				
habitat, FID	5	1064.77	2.41	0.01				
habitat*aggregation, habitat*sex, habitat*FID, predation(t-1)	11	1064.79	2.43	0.01				
aggregation, sex, FID, predation(t-1)	7	1064.82	2.46	0.01				

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sex, FID	5	1064.89	2.53	0.01
habitat, FID, predation(t-1)	6	1064.90	2.54	0.01

Site fidelity	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
habitat*aggregation, habitat*FID, habitat*predation(t-1)	10	1064.97	2.61	0.01				
habitat*aggregation, FID, breeding success(t-1)	7	1064.99	2.63	0.01				
habitat*aggregation, FID, productivity(t-1)	7	1065.04	2.68	0.01				
aggregation, sex, FID	6	1065.13	2.77	0.01				
habitat, sex, FID	6	1065.28	2.92	0.01				
habitat, sex, FID, predation(t-1)	7	1065.36	3.00	0.01				
habitat*aggregation, sex, FID, breeding success(t-1)	8	1065.41	3.05	0.01				
habitat*aggregation, sex, FID, productivity(t-1)	8	1065.46	3.10	0.01				
habitat, sex	5	1065.50	3.14	0.01				
sex, habitat*FID, habitat*predation(t-1)	9	1065.50	3.14	0.01				
habitat, aggregation, sex	6	1065.51	3.15	0.01				
habitat	4	1065.57	3.21	0.01				
habitat, aggregation	5	1065.58	3.22	0.01				

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habitat, aggregation, FID, breeding success(t-1)	7	1065.60	3.24	0.01
habitat*aggregation, habitat*FID, habitat*productivity(t-1)	9	1065.65	3.29	0.01

Site fidelity	k	AICc	ΔAICc	weight	Variables	Estimate	2.5%	97.5%
habitat, aggregation, FID, productivity(t-1)	7	1065.70	3.34	0.01				
aggregation, habitat*sex, FID, predation(t-1)	9	1065.73	3.37	0.01				
habitat, aggregation, sex, predation(t-1)	7	1065.80	3.44	0.01				
aggregation, FID, habitat*predation(t-1)	8	1065.81	3.45	0.01				
habitat, sex, predation(t-1)	6	1065.83	3.47	0.01				
aggregation, habitat*sex, FID	8	1065.84	3.48	0.01				
aggregation, habitat*FID, habitat*breeding success(t-1)	9	1065.92	3.56	0.01				
habitat, aggregation, predation(t-1)	6	1065.96	3.60	0.01				
habitat, predation(t-1)	5	1065.99	3.63	0.01				
aggregation, habitat*FID, habitat*productivity(t-1)	8	1066.00	3.64	0.01				
sex, habitat*FID, habitat*productivity(t-1)	8	1066.04	3.68	0.01				
aggregation, habitat*sex, habitat*FID, breeding success(t-1)	10	1066.12	3.76	0.01				
habitat, aggregation, sex, FID, breeding success(t-1)	8	1066.22	3.86	0.00				

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aggregation, habitat*sex, habitat*FID, productivity(t-1)	10	1066.24	3.88	0.00
FID, breeding success(t-1)	5	1066.27	3.91	0.00

Site fidelity	k	AICc	ΔAICc	weight	Variables	Estimate	2.5%	97.5%
habitat, aggregation, sex, FID, productivity(t-1)	8	1066.32	3.96	0.00				
FID, productivity(t-1)	5	1066.34	3.98	0.00				
aggregation, FID, breeding success(t-1)	6	1066.44	4.08	0.00				
habitat*aggregation, habitat*sex, habitat*FID, breeding success(t-1)	11	1066.44	4.08	0.00				
habitat*aggregation, habitat*FID, habitat*breeding success(t-1)	10	1066.45	4.09	0.00				
aggregation, FID, productivity(t-1)	6	1066.50	4.14	0.00				
habitat*aggregation, habitat*sex, habitat*FID, productivity(t-1)	11	1066.55	4.19	0.00				
habitat*sex	6	1066.55	4.19	0.00				
aggregation, habitat*sex	7	1066.59	4.23	0.00				
habitat, FID, breeding success(t-1)	6	1066.59	4.23	0.00				
habitat*sex, FID	7	1066.63	4.26	0.00				

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habitat*sex, FID, predation(t-1)	8	1066.63	4.27	0.00				
habitat, FID, productivity(t-1)	6	1066.69	4.33	0.00				
Site fidelity	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
aggregation, habitat*sex, predation(t-1)	8	1066.77	4.41	0.00				
habitat*sex, predation(t-1)	7	1066.78	4.42	0.00				
sex, FID, breeding success(t-1)	6	1066.78	4.42	0.00				
sex, FID, productivity(t-1)	6	1066.85	4.49	0.00				
FID, habitat*predation(t-1)	7	1066.89	4.53	0.00				
habitat*aggregation, sex	6	1066.89	4.53	0.00				
aggregation, sex, FID, breeding success(t-1)	7	1067.02	4.66	0.00				
sex, habitat*FID, habitat*breeding success(t-1)	9	1067.07	4.71	0.00				
aggregation, sex, FID, productivity(t-1)	7	1067.08	4.72	0.00				
habitat, sex, FID, breeding success(t-1)	7	1067.11	4.75	0.00				
habitat*sex, habitat*FID, habitat*predation(t-1)	10	1067.16	4.80	0.00				
habitat, sex, FID, productivity(t-1)	7	1067.21	4.85	0.00				
habitat, aggregation, sex, breeding success(t-1)	7	1067.28	4.92	0.00				

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habitat*aggregation, sex, predation(t-1)	7	1067.28	4.92	0.00
habitat, sex, breeding success(t-1)	6	1067.29	4.93	0.00

Site fidelity	k	AICc	ΔAICc	weight	Variables	Estimate	2.5%	97.5%
habitat, aggregation, breeding success(t-1)	6	1067.34	4.98	0.00				
habitat, breeding success(t-1)	5	1067.35	4.99	0.00				
sex, FID, habitat*predation(t-1)	8	1067.36	5.00	0.00				
habitat, aggregation, sex, productivity(t-1)	7	1067.43	5.07	0.00				
habitat, sex, productivity(t-1)	6	1067.43	5.07	0.00				
aggregation, FID, habitat*breeding success(t-1)	8	1067.47	5.11	0.00				
habitat, aggregation, productivity(t-1)	6	1067.49	5.13	0.00				
habitat, productivity(t-1)	5	1067.50	5.14	0.00				
aggregation, habitat*sex, FID, breeding success(t-1)	9	1067.64	5.28	0.00				
habitat*aggregation, habitat*sex, habitat*predation(t-1)	10	1067.65	5.29	0.00				
habitat*aggregation	5	1067.72	5.36	0.00				
aggregation, habitat*sex, FID, productivity(t-1)	9	1067.75	5.39	0.00				
aggregation, sex, habitat*predation(t-1)	8	1067.79	5.43	0.00				

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sex, habitat*predation(t-1)	7	1067.80	5.44	0.00				
FID, habitat*productivity(t-1)	6	1067.87	5.51	0.00				
Site fidelity	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
habitat*predation(t-1)	6	1067.94	5.58	0.00				
aggregation, habitat*predation(t-1)	7	1067.94	5.58	0.00				
aggregation, FID, habitat*productivity(t-1)	7	1068.08	5.72	0.00				
habitat*aggregation, predation(t-1)	6	1068.20	5.84	0.00				
habitat*sex, habitat*FID, habitat*productivity(t-1)	10	1068.31	5.95	0.00				
habitat*sex, breeding success(t-1)	7	1068.32	5.96	0.00				
aggregation, habitat*sex, breeding success(t-1)	8	1068.34	5.98	0.00				
Dispersal distance	**k**	**AICc**	**ΔAICc**	**weight**	**Variables**	**Estimate**	**2.5%**	**97.5%**
habitat, breeding success(t-1)	6	447.20	0.00	0.32	**habitat(urban)**	**-0.28**	**-0.50**	**-0.06**
habitat*breeding success(t-1)	7	448.10	0.90	0.21	**breeding success(t-1)**	**-0.25**	**-0.46**	**-0.04**
habitat*breeding success(t-1)	7	448.10	0.90	0.21	breeding success(t-1)*habitat(urban)	0.21	-0.01	0.43
habitat, sex, breeding success(t-1)	7	449.26	2.07	0.12	**sex(female)**	**0.09**	**0**	**0.18**

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sex, habitat*breeding success(t-1)	8	450.36	3.16	0.07	**productivity(t-1)**	**-0.04**	**-0.06**	**-0.01**
habitat	5	452.80	5.61	0.02				
habitat, productivity(t-1)	6	453.07	5.88	0.02				

Table S3. Relative importance of an individual's traits (sex and behaviour, measured as FID), previous breeding experience (breeding success, productivity and predation in the previous year *t-1*) and conspecific density on the dispersal pattern (site fidelity and dispersal distances) of rural burrowing owls *Athene cunicularia* with FID within the range of urban ones (5- 87m). Estimates and 95% confidence intervals (2.5% and 97.5%) were assessed after model averaging. We considered that a given variable has no, weak or strong support when the 95% confidence interval strongly overlapped zero, barely overlapped zero, or did not overlap zero (in bold), respectively. Models shown are those used for model averaging (ΔAICc ≤ 6).

Site fidelity	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
FID	4	198.15	0.00	0.14	**FID**	**-0.38**	**-0.74**	**-0.01**
FID, productivity(t-1)	5	199.35	1.20	0.08	productivity(t-1)	-0.16	-0.5	0.19
FID, breeding success(t-1)	5	199.39	1.24	0.07	breeding success(t-1)	-0.35	-1.11	0.42
sex, FID	5	199.52	1.38	0.07	sex(female)	-0.34	-1.07	0.38
FID, predation(t-1)	5	199.62	1.47	0.07	predation(t-1)	-0.42	-1.57	0.73
aggregation, FID	5	199.84	1.70	0.06	aggregation	0.11	-0.24	0.45
sex, FID, breeding success(t-1)	6	200.71	2.56	0.04				
sex, FID, productivity(t-1)	6	200.71	2.57	0.04				

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Site fidelity	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
sex, FID, predation(t-1)	6	200.89	2.74	0.04				
aggregation, FID , productivity(t-1)	6	201.03	2.88	0.03				
aggregation, FID , breeding success(t-1)	6	201.07	2.92	0.03				
aggregation, sex, FID	6	201.15	3.00	0.03				
null	3	201.16	3.01	0.03				
aggregation, FID , predation(t-1)	6	201.42	3.27	0.03				
sex	4	201.45	3.30	0.03				
aggregation, sex, FID, breeding success(t-1)	7	202.32	4.17	0.02				
aggregation, sex, FID, productivity(t-1)	7	202.33	4.18	0.02				
breeding success(t-1)	4	202.34	4.19	0.02				
productivity(t-1)	4	202.38	4.24	0.02				
aggregation	4	202.52	4.37	0.02				
sex, breeding success(t-1)	5	202.56	4.41	0.02				

*Continues on the next page

Site fidelity	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
predation(t-1)	4	202.57	4.43	0.02				
aggregation, sex, FID , predation(t-1)	7	202.63	4.49	0.01				
sex, productivity(t-1)	5	202.65	4.51	0.01				
sex, predation(t-1)	5	202.70	4.55	0.01				
aggregation, sex	5	202.73	4.59	0.01				
aggregation, breeding success(t-1)	5	203.68	5.53	0.01				
aggregation, productivity(t-1)	5	203.73	5.58	0.01				
aggregation, sex, breeding success(t-1)	6	203.83	5.68	0.01				
aggregation, sex, productivity(t-1)	6	203.93	5.78	0.01				
aggregation, predation(t-1)	5	204.09	5.94	0.01				

Dispersal distance	df	BIC	ΔBIC	weight	Variables	Estimate	2.5%	97.5%
breeding success(t-1)	5	101.85	0.00	0.82	**breeding success(t-1)**	**-0.40**	**-0.60**	**-0.20**
sex, breeding success(t-1)	6	106.52	4.67	0.08	sex(females)	0.05	-0.14	0.23

2. Estimating personality-related resighting rates

We have analyzed capture-recapture data on breeders for which FID is available. First, we have modeled survival by keeping recapture as general as possible (Table S4). Then, once the structure of survival that minimizes AIC was selected (i.e. a model including temporal variation but not differences between habitats or sexes), we have modeled recapture probabilities (Table S5). The best model indicates a sex effect on recapture probabilities, with higher recapture probabilities for males (Table S6). Moreover, the second best model indicates that habitat effects in interaction with sex could be a good predictor of recapture probabilities but not habitat per se (Table S5). In fact, females at rural areas show the lowest recapture probabilities (Table S7; it is important to mention this "lower" recapture probability is very high).

Table S4. Modelling the effects of time (t), habitat (HAB) and sex (SEX) on survival. k: number of parameters estimated by the model.

MODEL	SURVIVAL	RECAPTURE	AICc	ΔAICc	K	Deviance
1	TIME	SEX*HAB*t	1380.0701	0	38	1301.2036
2	HAB*TIME	SEX*HAB*t	1380.6167	0.5466	45	1286.5855
3	HAB	SEX*HAB*t	1383.0726	3.0025	33	1314.9128
4	SEX*HAB	SEX*HAB*t	1387.1559	7.0858	35	1314.7258
5	CONSTANT	SEX*HAB*t	1387.9109	7.8408	32	1321.8801
6	SEX*t	SEX*HAB*t	1388.7391	8.669	45	1294.7079
7	SEX	SEX*HAB*t	1389.882	9.8119	33	1321.7222
8	SEX*HAB*t	SEX*HAB*t	1400.964	20.8939	58	1278.2145

Table S5. Modelling the effects of time (t), habitat (HAB) and sex (SEX) on recapture using a time-dependent survival structure (see Table S4). k: number of parameters estimated by the model.

MODEL	SURVIVAL	RECAPTURE	AICc	ΔAICc	k	Deviance
1	TIME	SEX	1351.0634	0	10	1330.8562
2	TIME	SEX*HAB	1353.258	2.1946	12	1328.9637
3	TIME	CONSTANT	1356.3104	5.247	9	1338.1411
4	TIME	HAB	1357.9279	6.8645	10	1337.7207
5	TIME	TIME	1359.2953	8.2319	15	1328.8412
6	TIME	SEX*t	1360.1389	9.0755	23	1313.0865
7	TIME	HAB*TIME	1367.5309	16.4675	23	1320.4785
8	TIME	SEX*HAB*t	1380.0701	29.0067	38	1301.2036

Table S6. Estimates and 95% conFIDence intervals (LCI: 2.5% and UCI: 97.5%) of recapture probabilities based on the model SURVIVAL(t), RECAPTURE(sex) (Model 1, Table S5).

Recapture	Estimate	SE	LCI	UCI
Males	0.976	0.009	0.949	0.989
Females	0.928	0.015	0.892	0.953

Table S7. Estimates and 95% conFIDence intervals (LCI: 2.5% and UCI: 97.5%) of recapture probabilities based on the model SURVIVAL(t), RECAPTURE(sex*habitat) (Model 2, Table S5).

Recapture	Estimate	SE	LCI	UCI
Males Urban	0.972	0.012	0.935	0.988
Females Urban	0.940	0.017	0.897	0.965
Males Rural	0.987	0.013	0.912	0.998
Females Rural	0.900	0.032	0.817	0.948

Regarding the potential effects of FID on recapture rates, we did not find any relationship (Table S8 and S9). All the 95%CI of the beta estimates of FID included zero, indicating a lack of significant effects of individual's personality on recapture probabilities (Table S9).

Table S8. Testing the effect of an individual's personality (FID), sex (SEX) and habitat (HAB) on recapture probabilities using a time-dependent survival structure (see Table S4). k: number of parameters estimated by the model.

Model	SURVIVAL	RECAPTURE	AICc	ΔAICc	k	Deviance
1	TIME	SEX	1351.0634	0	10	1330.8562
2	TIME	SEX*FID	1354.0572	2.9938	12	1329.7629
3	TIME	FID	1357.0177	5.9543	10	1336.8105
4	TIME	HAB*FID	1360.5552	9.4918	12	1336.2609
5	TIME	SEX*HAB*FID	1360.7111	9.6477	16	1328.1959

Table S9. Estimates and 95% confidence intervals (LCI: 2.5% and UCI: 97.5%) for the effect of individual's personality (FID) on recapture probabilities (based on models presented in Table S8).

Model	Parameter	Estimate	LCI	UCI
2	slope FID males	0.0058866	-0.04005	0.0518231
2	slope FID females	-0.0066979	-0.0180615	0.0046657
3	slope FID	-0.0075621	-0.0187288	0.0036047
4	slope FID urban	0.01136	-0.0408484	0.0635684
4	slope FID rural	-0.0084598	-0.0213536	0.0044341
5	slope FID urban males	0.0058557	-0.098415	0.1101264
5	slope FID urban females	0.0171106	-0.0428763	0.0770976
5	slope FID rural males	-0.0039968	-0.0603889	0.0523953
5	slope FID rural females	-0.0050906	-0.019355	0.0091737

IV| Epilogue

General discussion

General discussion

Connecting urban ecology with dispersal

The footprint of urban areas continues to expand worldwide, giving the growing proportion of humans abandoning rural areas to settle in cities (McKinney, 2002; Grimm et al. 2008). Today we know that urbanization deeply affects ecological processes and animal behaviors (Ditchkoff et al. 2006; Devictor et al. 2007; Kareiva et al 2007*;* Aronson et al. 2014; Lapiedra et al. 2016). Among the possible effects detected on animals, some evidences suggest that their space use and movements could be altered in urbanized areas (Markovchick-Nicholls et al. 2008; Munshi-South and Nagy 2014). In this sense, different studies have indicated how flight decisions of migrating birds are impacted by artificial lights or by the air temperature of cities (Van Doren et al. 2017; Cabrera-Cruz et al. 2019), and how the urban environment can alter the home range size of different species (Vangestel et al. 2010; Lowry et al. 2013). However, to the date ecologists still lack evidence of the underlying mechanisms that may alter dispersal strategies in urbanized areas, as well as the potential consequences derived from this. Indeed, to the best of my knowledge, no previous thesis has focused specifically in dispersal strategies of species inhabiting urban and rural habitats.

My thesis demonstrates how dispersal decisions of a small owl can vary between individuals inhabiting zones as different as one city and their rural surrounding. An overview of my results indicates that dispersal decisions depend primarily on the inter-individual variability in personality traits related to the susceptibility to human disturbances (**Chapters I and III**). Moreover, the spatial heterogeneity in selective pressures (e.g. predators) existent in both habitats and even within them affects the dispersal of burrowing owls. Some consequences related to dispersal decisions are evident in two main fitness components: primarily in fecundity and to a lesser extent in local survival (**Chapters I and II**).

Attending to the results obtained, this thesis highlights that burrowing owls generally disperse short distances (or directly remain in the same territory) (**Chapters I, II and III**). The great majority of dispersal events recorded in this study covered less than 1 kilometer. This confirms that moving to unknown areas is not the preferred strategy for the species in the study area. Furthermore, in agreement with general knowledge, the propensity to disperse tends to decrease with the age, as they gain experience as breeders (Greenwood and Harvey 1982; Paradis et al. 1998) (**Chapters I and III**). In this sense, burrowing owls in Bahía Blanca area disperse longer distances when juveniles (i.e. natal dispersal, **chapter I**) than once they become breeders (i.e. breeding dispersal, **chapter III**). A deeper approach to the results show that 25% of young burrowing owls dispersing for first time settled at > 1000 meters from the natal nest while only 1.2% of adults dispersed at >1000 meters between breeding events. A small portion of juveniles (9.5%) not even change from another territory, remaining in their natal nest. This proportion grow for experienced adults (47.9%), revealing a growing faithful to the breeding territory between years.

The sex also played a role in the dispersal strategies of burrowing owls. In general, females disperse farther distances than males, which is in accordance with the observed pattern in birds (Greenwood 1980; Clarke et al. 1997) (**Chapters I and III**). For young females dispersing for first time the median dispersal distance was approximately 1681 meters, while for males was 554 meters. The same fact is maintained for experienced adults, although with lower distances (median males ~75 meters; median females ~ 45 meters). The low dispersal propensity detected in males may also explain why in the 98% of cooperative breeding events the third adult was a male (**Chapter II**). A possible explanation to the site fidelity showed by males may rely in potential advantages obtained by the familiarity to the territory for this sex (i.e. attract a mate and breed successfully) (Pärt 1995; Piper et al. 2008). However, to explain female- biased dispersal other non-exclusive hypotheses have been also considered. Thus, females may disperse longer distances to avoid reproduction between relatives and diminish resource and intrasexual competition for males (Perrin and Mazalov 2000). The habitat plays a central role in this thesis: urban burrowing

owls disperse less frequently and move shorter distances than their rural counterparts (**Chapters I, II and III**). This result does not support the idea that urban individuals necessarily have to disperse more than their rural conspecifics (Møller 2009), but expand the previous hypothesis with an example based in continuous monitoring of a species. Urban juveniles disperse a median of 1192 meters while rural 1175 meters. Moreover, in the 39% of breeding events recorded in rural areas the adults were faithful to their nest, while this percentage rises until 50% in the city. Curiously, in juveniles the site fidelity is less frequent but they develop two ways of non- dispersal strategy: they can inherit the birth territory if their relatives die or disperse, but they can even delay their dispersal to collaborate in reproductive tasks with their relatives, forming cooperative breeding structures (Cockburn, 2006) (**Chapters I and II**). These atypical breeding structures (trios and quartets) are more common also in the city. Although breeding dispersal distances were especially short, it was possible to observe slight differences between habitats: the median for breeding dispersal distances was around 100 meters for rural and 76.5 for urban individuals.

Table 1.Summary of the main biological questions and results obtained in this thesis.

Chapter	Topic	Biological question	Main results
1	**Natal dispersal**	What individual and social factors can influence natal dispersal distances?	Urban burrowing owls disperse shorter distances. Females, bold and individuals born in less densely inhabited areas disperse far distances
		Do dispersal decisions have reproductive and survival consequences?	Positive reproductive consequences in urban and rural burrowing owls Females dispersing farther show lower local survival
2	**Cooperative breeding (by delayed dispersal)**	Kinship and parentage of adults and offspring involved in cooperative breeding events	The extra adults are young males that delay dispersal.
		What ecological conditions promote the development of cooperative breeding?	Habitat quality and changes associated to urbanization
		Role played by the helper	Food provisioning,
		Does cooperative breeding play a role in reproductive parameters and the survival of the offspring?	Cooperative breeding improve reproductive parameters but not specially the offspring survival
3	**Breeding dispersal**	What are the individual and social factors that influence site fidelity and breeding dispersal distances in urban and rural burrowing owls?	Site fidelity among rural birds was lower and they disperse longer distances. Rural dispersal related to fear of humans and previous experience in a territory. Urban individuals breeding at dense aggregations are prone to disperse.

Fear of humans and dispersal in urban versus rural habitats

Fear of humans is included within a range of behavioral traits that often co-occurs at individual level, encompassing risk taking, shyness, reaction to novelties, aggressiveness, and dispersal and exploration propensity (Fraser et al. 2001; Dingemanse et al. 2003; Sih and Bell 2008; Evans et al. 2010). In recent years it has been suggested that these interrelated behaviors play an important role in the colonization of urban environments, with bold individuals being more prone to explore and settle in human dominated areas (Møller 2010). This is the case of the studied species, whose distribution has been demonstrated to respond to the individual susceptibility of humans (Carrete and Tella 2011). Indeed, the urban population is mainly composed by bold individuals that tolerate human presence and its associated activities (Carrete and Tella 2010; Rebolo-Ifrán et al. 2015).

Few studies have simultaneously evaluated how potentially correlated factors, such as behavioral and dispersal, respond to the anthropization of the landscape. My results support the idea that dispersal strategies in this species are influenced by the temperament of each individual, measured through the fear of humans (**Chapters I and III**). In the study area, juvenile bold burrowing owls inhabiting both habitats disperse farther from their natal nest than shy individuals. On the contrary, bold breeding adults at rural areas are less prone to disperse, and they do at shorter distances while breeding adults at urban areas do not show differences in their dispersal decisions related with their boldness.

Personality tends to be consistent across life (Réale et al. 2007; Carrete and Tella 2010). However, personality related behavioral traits can be expressed in different ways among diverse contexts, and according with the experience of the individual (Sih et al. 2004a; Sih et al. 2004b). This could explain the differences in the effect of boldness on the dispersal pattern of juvenile and adult burrowing owls between habitats. Bolder juveniles may have higher exploration capabilities (Fraser et al. 2001). On the contrary, bold experienced adults may be more tolerant to disturbance and

remain faithful to their territory despite possible adverse circumstances (**Chapter III**). In fact, at the city, were most of the individuals are bold, no effect of personality in dispersal was observed and dispersal probabilities and distances were especially low. The enemy- release and the homogeneous selective pressures associated to the city can dilutes the role of the personality, linking breeding dispersal decisions of urban burrowing owls to other factors. At rural areas, individuals are more heterogeneous in their personality traits and shy individuals may be especially susceptible to disturbances as the ones caused by predator presence, thus dispersing higher proportions and distances when conditions are adverse.

Social factors influencing dispersal decisions

The different chapters included in this thesis highlight the key role of habitat features on dispersal decisions. The existence of patches with different quality affects the spatial aggregation of the burrowing owls, and hence their dispersal decisions. Moreover, burrowing owls use social information (mainly the conspecific density) as cues for habitat quality assessment and breeding habitat selection, in agreement with previous research on other bird species (Davis and Stamp 2004; Doligez et al. 2004; Serrano et al. 2003; Matthysen, 2005).

In this sense, juveniles born in good quality patches (that also have high conspecific density) may be reluctant to move to unfamiliar areas, reducing the cost associated to dispersal (Bonte et al. 2012) (**Chapter I**). This also explains why burrowing owls raised in better quality patches even choose to cooperate with their parents instead of dispersing and breeding independently (Komdeur 1992; Hatchwell and Komdeur 2000) (**Chapter II**).The success of this philopatric strategy makes sense in this species because of their short lifespan. By remaining at the natal area individuals may acquire a high quality territory access in a short time. As example, males that forgo their reproduction to help their parents can inherit the natal territory or settle close, but always in familiar areas. On the other side, individuals born in low quality areas where breeding success is lower may try to disperse and settle in better places (Boulinier et al.2002;

Payo-Payo et al. 2018). In this thesis, settlement decisions may be done based on conspecific density and breeding success (**Chapters I, II and III**). Thus, adults disturbed by predators and/or that failed in reproduction were more prone to disperse, confirming the tendency to avoid bad quality territories detected in other studies (Serrano et al. 2001; Pasinelli et al. 2007). However, an apparently paradoxical situation appears in urban environments. Instead of trying to breed close, adults nesting in high density patches disperse farther from their conspecifics than individuals breeding in low dense urban areas (**Chapter III**). Although dense aggregations of individuals can indicate a high quality of the habitat, high conspecific density also implies competitive interactions (Forero et al. 2002). In the city predator pressure is especially low and breeding success is high (Rebolo- Ifrán et al. 2017). Urban adults may disperse from dense areas in higher proportions than in rural birds to avoid intraspecific competition because by settle in a new urban territory the chances of breeding successfully may continue being high.

Consequences of dispersal decisions in reproductive and survival parameters

Habitat heterogeneity has been demonstrated to have an important effects at both individual and population level (Ibañez-Álamo and Soler 2010). In this sense, the decisions on where to settle can be vital for individuals, but travel associated to disperse can entail negative consequences, which can counteract the possible benefits of such decisions (Bonte et al. 2010; Tarwater et al. 2010). Understanding the fitness consequences of dispersal for a species inhabiting urban and rural habitats may be of special interest in humanized areas. In this respect, it is necessary to study the role that dispersal decisions can have in reproductive and survival parameters (Bowler and Benton 2005; Doligez and Pärt 2008; Nevoux et al 2013). In this study area, selective pressures in the city are drastically different compared to those that burrowing owls cope in their original habitat (e.g. predators). Indeed, in Bahía Blanca urban burrowing owls have better reproductive parameters (Rebolo-Ifrán et al. 2017 and this thesis).

In the case of burrowing owls the consequences are mainly related to natal dispersal (both for dispersers and for non- dispersers) (**Chapters I and II**), while neither reproductive nor survival relation was detected in subsequent dispersal decisions. Specifically, my results show that females and rural individuals dispersing longer distances from their natal nest produce more offspring in their first breeding attempt , and higher reproductive success appear in individuals inhabiting the two habitats when consider their entire life (**Chapter I**). Curiously, the territories that develop cooperative breeding also have more reproductive success and the offspring raised in such family structures have better body condition (**Chapter II**), showing a possible advantage of non- dispersal strategies (Woxvold and Magrath 2005; Kingma et al. 2010).

However, the benefits in term of reproduction may be hampered by the costs of dispersal. In the study area, the survival of adult is high compared to those of the juveniles, which differ between habitats, with urban juveniles showing better survival prospect than rural (**Chapter II**). A plausible explanation emerge from these results: rural individuals are more prone to disperse, so the lower survival of dispersers may rely in cost associated to natal dispersal decisions. Once the individuals have experience (they have survived 1st year) the differences between habitats disappear, although they may exist in especially bad years (Rebolo-Ifrán et al. 2015). However, the differences between juveniles and adults survival may arise due to ecological factors per se, as predators and food availability, which affect especially to younger (inexperienced) individuals (Wiens et al. 2006; Seward et al. 2013). The results shown in this thesis reveal that survival seems related more to the natal dispersal; in fact, neither negative nor positive effect of breeding dispersal in survival was detected. Females that settled at higher distances from their natal nest showed lower local survival than females remaining close to their natal territory (**Chapter I**), as observed in other birds (Nevoux et al. 2013). Contrarily, a slight positive effect in the survival of chicks raised in cooperative breeding families was detected, suggesting a possible gain of site fidelity showed by helpers.

Sadly, during the fieldwork were only detected live individuals. Consequently, was impossible to assess how dispersal decisions could affect post-fledgling survival, because we don't have information about where undetected young burrowing owls try to settle, or what decisions took during their first year. Moreover, the monitoring program is conducted from October to February, so there is certainty about where the individuals were finally settled during the breeding season, but not about their movements during the whole year (the total distances traveled until finally settling in a specific territory, the moment at which they start to search for breeding territories, or how they prospect the different habitats and/or patches within them). To obtain this information, my thesis included the marking of individuals with GPS, but this chapter was finally ruled out due to different logistic complications that made impossible to obtain the spatial data at time for my thesis.

Urban colonization and the population structure of the burrowing owl

In order to understand the colonization process started some decades ago, studying how animal disperse is essential. First, for a part of the rural population the city is outside their probable range of dispersal. The remoteness of a part of the rural territories to the city difficult this colonization, more when consider the low propensity to disperse longer distances showed by the studied species. Moreover, although some rural individuals breeding near the city have major possibilities to explore the urban habitat, those that are naturally timid or neophobic could be precluded to successfully settle in this human dominated area (Møller 2010, Carrete and Tella 2017), hence reducing the possibilities to move to these zones. This help to explains the low number of individuals that have changed from urban to rural habitats -and vice versa- across this long term monitoring (Mueller et al. 2018). As a consequence, the predominant short dispersal distances together with the reduced gene flow favor -in absence of geographic or physical barriers- the population differentiation at small spatial scale. All together support the information recently provided by genetic procedures (Mueller et al. 2018), that coincide with the explanations offered for other recent urban

colonizations (Evans et al. 2009; Rutkowski et al. 2010): a limited number of founders from the rural environment settled in the city in recent times; there is hardly exchange of individuals between the two adjacent habitats, hence the restricted gene flow detected in urban and rural populations and the urban-rural population structure observed.

It is very likely that the dispersal patterns described here can be extended to other urban-rural areas. However, beyond the results obtained in my thesis is important to emphasize the fact that urban environments are really varied throughout the world: every city has their structure, ecological conditions and level of human disturbance. Similarly, behavioral differences present in each species (Hodgson et al. 2007) and even among populations (Rodewald and Shustack 2008) leads us to think that there must be different dispersal responses of birds respect to urbanization. The conclusions drawn from my work offer novel perspectives, but would be reinforced and expanded if more research were conducted. Thus, I consider that this work can stimulate others to study dispersal in urban environments.

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Conclusiones generales
General conclusions

Conclusiones generales

1. La lechucita de las vizcacheras generalmente dispersa distancias cortas o permanece fiel a un mismo territorio. Dispersar a áreas desconocidas no parece ser su estrategia predilecta. Hay jóvenes filopátricos que al no dispersar promueven el desarrollo de cría cooperativa (principalmente tríos), permaneciendo un año adicional en el territorio natal con sus progenitores.

2. La tendencia a dispersar decrece con la edad. En general, la dispersión natal incluye desplazamientos más largos que la dispersión reproductora. Además, los adultos experimentados son más fieles a un mismo territorio que los jóvenes.

3. Las hembras dispersan con mayor frecuencia, y cuando lo hacen cubren mayores distancias que los machos, tanto en la dispersión natal como en la reproductora. El hecho de que los machos sean menos propensos a dispersar ayuda a explicar que el adulto adicional cuando se forman tríos reproductores sea mayoritariamente de este sexo.

4. La dispersión varía entre hábitats. Las lechucitas rurales dispersan con mayor frecuencia y lo hacen a mayor distancia que las urbanas, tanto en la dispersión natal como la reproductora. Además, aparecen más casos de cría cooperativa por permanencia en el territorio natal de juveniles en la ciudad.

5. La susceptibilidad al ser humano influye en la dispersión. Este rasgo de comportamiento se vincula a la exploración, la toma de riesgos y la dispersión. Los jóvenes atrevidos (“bold”) dispersan más, posiblemente por ser más exploradores y dados a tomar riesgos. Al contrario, al examinar la dispersión reproductora, se observa que en entornos rurales (no en los urbanos) los individuos atrevidos son menos dados a dispersar. Estos individuos podrían ser

capaces de asumir riesgos permaneciendo en un mismo territorio, evitando así los potenciales costes asociados a la dispersión.

6. Las estrategias de dispersión de esta especie se ven influenciadas por la calidad del hábitat variando entre juveniles y adultos. Los juveniles nacidos en territorios de mayor calidad (con mayor densidad de congéneres y éxito reproductor) dispersan menos y desarrollan con más probabilidad cría cooperativa. Por el contrario, los adultos reproductores de zonas urbanas con alta densidad de congéneres dispersan más lejos, probablemente para reducir la competencia intraespecífica.

7. El efecto de la dispersión en el éxito reproductor varía por género y hábitat. Las hembras e individuos rurales que dispersan lejos de su territorio natal mejoran su productividad reproductora en el primer año. Este efecto se extiende a ambos sexos y hábitats al considerar el éxito reproductor a lo largo de la vida. Por otro lado, los nidos con cría cooperativa producen más pollos y en mejor condición física.

8. En algunos casos los beneficios asociados a la dispersión podrían anularse debido a los costes en términos de supervivencia. Así, la supervivencia aparente de las hembras decrece a mayor distancia de dispersión recorrida. Sin embargo, no se detectan importantes diferencias de supervivencia relacionadas con la dispersión o el nacimiento en un territorio regentado por una pareja o más de dos adultos.

9. Esta tesis pone de relieve la importancia de desarrollar programas de monitoreo a largo plazo a nivel individual y poblacional, más si cabe en ciudades, donde este tipo de proyectos escasean. La información obtenida es crucial para comprender los procesos de colonización y la dinámica poblacional de especies que habitan áreas urbanas y rurales.

General conclusions

1. Burrowing owls generally disperse short distances or directly remain faithful to the same territory. Disperse to unfamiliar areas is not the predominant strategy for the species in the study area. There are philopatric juveniles that do not disperse, promoting the development of cooperative breeding strategies (mainly trios), remaining one additional year in their natal territories with their parents.

2. Dispersal propensity tends to decrease with the age. In general, natal dispersal includes longer displacements than breeding dispersal. Moreover, more experienced adults are more faithful to a same territory than juveniles.

3. Females disperse more frequently, and when disperse they cover longer distances than males, both in natal and breeding dispersal. The lower dispersal propensity detected in males may help to explain why the extra adults collaborating in cooperative breeding systems are mostly young males.

4. Dispersal decisions vary between habitats. Rural burrowing owls disperse more frequently and disperse longer distances than their urban counterparts. Furthermore, cooperative breeding by delayed dispersal of juveniles that remain in the natal area is more frequent in the city.

5. The susceptibility to humans influences dispersal strategies. This behavioral trait is related to exploration, aggressiveness and dispersal. Bold young burrowing owls disperse farther from their natal territory, probably to be more explorative and risk-takers. On the contrary, when consider breeding dispersal, in rural habitats (not in urban ones) the bold individuals are less prone to disperse. These individuals may be able to take risks while remaining in the same territory, thus avoiding the potential costs associated with dispersal.

6. Dispersal decisions of this species are influenced by habitat quality, varying between juveniles and adults. Juveniles born in high quality patches (with higher density of conspecifics and reproductive success) disperse less and develop cooperative breeding with higher frequency. In contrast, adult breeders in urban areas with high density of congeners disperse farther, probably to reduce intraspecific competition.

7. The effects of dispersal on reproductive success vary by sex and habitat. Females and rural individuals settling far from their natal territories improve their productivity in their first breeding attempt. This extends to both sexes and habitats when consider the reproductive output throughout the entire life. Burrowing owls developing cooperative breeding also have more reproductive success, raising chicks with better body condition.

8. In some occasions the reproductive gains associated with dispersal may be hampered by its survival costs. Thus, the apparent survival of females decreases when they disperse longer distances. However, we don't detect significant survival differences related to the number of adults collaborating in reproductive tasks in a same nest.

9. This thesis emphasizes the importance to develop long- term monitoring programs at individual and population level, especially in cities, where these projects are scarce. The information obtained is crucial to understand urban colonization processes and population dynamics of species in urban and rural areas.

Publications summary

Publications summary

Papers in JCR indexed journals

Accepted publication included in this thesis:

Luna Á, Palma A, Sanz-Aguilar A, Tella JL, Carrete M. Personality-dependent breeding dispersal in rural but not urban burrowing owls. Scientific reports. 2019; 9(1), 2886.

Apart from the contents included in this thesis I have a more extensive scientific output derived from parallel collaborations. These publications are also focused in urban ecology, but exploring different aspect related to urban birds: social perception, colonization of invasive species, and conservation of endangered species in cities.

- **Luna Á**, Edelaar P, Shwartz A (2019). Assessment of social perception of an invasive parakeet using a novel visual survey method. NeoBiota, 46, 71.

- **Luna Á**, Romero-Vidal P, Hiraldo F, Tella JL (2018). Cities may save some threatened species but not their ecological functions. PeerJ, 6, e4908.

- **Luna Á**, Romero-Vidal P, Hiraldo F, Tella JL(2018).. Cities favour the recent establishment and current spread of the Eurasian collared dove Streptopelia decaocto (Frivaldszky, 1838) in Dominican Republic. Bioinvasion Records, 7.

- **Luna Á**, Franz D, Strubbe D, Shwartz A, Braun MP, Hernández-Brito D ... & van Turnhout CA (2017). Reproductive timing as a constraint on invasion success in the Ring-necked parakeet (Psittacula krameri). Biological Invasions, 19(8), 2247-2259.

- Turbé A, Strubbe D, Mori E, Carrete M, Chiron F, Clergeau P , González-Moreno P, Le Louarn M, **Luna Á**, Menchetti M, Nentwig W, Pârâu L, Postigo JL, Rabitsch W, Senar JC, Tollington S, Vanderhoeven S, Weiserbs A, Shwartz A (2017). Assessing the assessments: evaluation of four impact assessment protocols for invasive alien species. Diversity and Distributions, 23(3), 297-307.

- **Luna Á**, Monteiro M, Asensio-Cenzano E, & Reino L (2016). Status of the rose-ringed parakeet Psittacula krameri in Lisbon, Portugal. Biologia, 71(6), 717-720.

- Pârâu L, Strubbe D, Mori E, Menchetti M, Ancillotto L, van Kleunen A, White R, **Luna Á**, Hernández-Brito D, LeLouarn M, Clergeau P, Albayrak T, Franz D, Braun MP, Schroeder J, Wink M (2016). Rose-ringed Parakeet Psittacula krameri populations and numbers in Europe: a complete overview. The Open Ornithology Journal, 9(1).

- Hernández-Brito D, **Luna Á**, Carrete M & Tella JL (2014). Alien rose-ringed parakeets (Psittacula krameri) attack black rats (Rattus rattus) sometimes resulting in death. Hystrix, the Italian Journal of Mammalogy, 25(2), 121-123.

Books

During my predoctoral period I focused part of my time off in other activities related with science. During the Summer of 2017 I published my first scientific divulgation book, “Un leopardo en el jardín” (Tundra Ediciones), finalist of the Prismas Award as Best Book of the year. My second book, “La era del plástico” will be launch in November 2019.

Press releases

La peculiar conservación de dos loros dominicanos (2019). Revista Quercus

Gestión de especies invasoras: la importancia de evaluar la percepción social (2019). Web Ecomandanga.

Ciudades: ¿el último refugio de las aves amenazadas? (2019). Web Birding 140.

Siguiendo a la tórtola turca en República Dominicana. (2018) Revista Quercus.

¿Qué especies conviven con los humanos en ciudades? (2018). Web La Caixa.

Científicos estudian las lechuzas urbanas de Bahía (2017) Boletín de la Universidad Nacional del Sur (Argentina).

Lo urbano les sienta bien. Estudio sobre lechucitas en Bahía Blanca (2017). Boletín Aves Argentinas.

V | Agradecimientos

Agradecimientos

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